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BIOLOGY OF THE SOUTHERN LYCTUS BEETLE, LYCTUS PLANICOLLIS[1]

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ABSTRACT

New techniques, described here, permitted more detailed studies of the biology of this powder-post beetle than were possible previously. Among these was one using wood shavings as an oviposition site from which large numbers of eggs could easily be collected. In several tests egg production averaged 51 per female; these were deposited over periods ranging up to 16 or 17 days, and more than 90% were viable. Incubation required about 8 days. Technical difficulties prevented determining the duration of larval life. A prepupal stage, previously unreported, preceded the pupal stage, which required about 8 days. An estimated period of 14 to 18 days elapsed after eclosion before adults constructed exits from the wood, and usually several more days passed before they actually emerged. The total duration of adult life averaged 33 days for males, 35 days for females. The sex ratio of 3,408 beetles maturing in a stock culture was 1,723 males to 1,685 females.

Relatively little detailed information on the various stages of the southern lyctus beetle, *Lyctus planicollis* LeConte, is found in the literature. Methods employed by workers in the past for securing eggs were very slow and tedious, and were accompanied by a high mortality rate. Alston (1923) estimated that, on an average, 75 percent of the eggs were lost in trying to locate them, and probably 60 percent of those located were damaged or destroyed in the endeavor to extract them from the vessels of the wood.

Christian (1940) indicated that the egg stage lasted 6 to 15 days. Smith (1956b) verified this, and added a brief description of the development of the embryo in the egg. The manner of hatching was described by Snyder (1916). Christian (1940) reported that the larval stages lasted from 4 to 9 months, and that the larvae remained quiet after completing the pupal chamber and underwent a gradual change into the pupal stage. He found that pupae of *L. planicollis* and of *Trogoxylon parallelopipedum* (Melsh.), which he studied together, remained inactive in their cells for a period of 12 days to 3 weeks, then changed to adults. Gerberg (1957) reported that the pupal period of *Lyctus* spp. lasted from 12 days to 1 month, and that the beetle cut its way to the surface when transformation from pupa to adult was completed. Christian (1941) said that a few beetles completed their life cycle in 4 to 5 months under favorable conditions, but development usually required a longer period. He had noted earlier (1940) that adults of *Lyctus planicollis* mated shortly after emergence and the females began to lay eggs, inserting them to a depth of 4 to 7.5 mm. in the wood. Snyder (1916) first reported that the eggs of this species were deposited into the open ends of pores of longitudinal vessels in the wood. He also mentioned that there was considerable preliminary examination of all parts of the pore with a pair of lateral palpi found at the extremity of the ovipositor, and that several eggs could be inserted into one pore.

Though Smith (1956b) made detailed studies on the oviposition of *Lyctus planicollis*, he obtained no extensive data on the oviposition potential of the females. His few observations showed a range of from 30 to 80 eggs per female, with viability of these eggs almost 100 percent. Christian (1940), considering *L. planicollis* and *Trogoxylon parallelopipedum* together, stated that the counts of offspring (larvae) of a known number of "mother beetles" indicated that each female laid about 25 fertile eggs, and that the adult life span lasted 3 to 4 weeks.

MATERIALS AND METHODS

Rearing of the southern lyctus beetle was done by the method outlined by Smith (1956a), except for the following modifications. All rearing and testing were done in a laboratory maintained at 31° ± 3° C. and 85% ± 5% R.H. Red-oak limbwood, either air-dried or oven-dried at 120° C., was used in the experiments.

Wood-shavings Technique.—This new technique was developed for securing large numbers of eggs.

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Shavings were cut from air-dried red oak with a jointer set at ¼ inch. These shavings were placed in water for approximately ½ minute, then were transferred to an embryological watch glass 1½ inches square, with concavity 1¼ inches in diameter by approximately 7/64 inch deep. After the shavings were tightly packed to within ¼ inch of the rim, a No. 18 cork was placed over the shavings and pressed down into the cavity. Several tight-fitting rubber bands, put over the cork and the watch glass, exerted sufficient pressure to keep the shavings compressed. The packed shavings were dried for 1 to 2 days at 120° C.; then, after cooling, the rubber bands and cork were removed and the watch glass containing the shavings (fig. 1) was placed in the laboratory.

FIG. 1.—An embryological watch glass containing red-oak wood shavings suitable for egg deposition by *Lyctus planicollis* females.

Male and female beetles were placed on the shavings in the watch glass and were allowed to mate. A cover glass, 35 x 50 mm., placed over the watch glass cavity and held in place by a rubber band, prevented their escape while an experiment was in progress. At the end of a test the adults were removed, and the chips were carefully examined under 18x magnification for eggs, or for young larvae. Eggs were removed from the shavings with a small camel's-hair brush, or with a dissecting needle. Those appearing shrunken, shriveled, or misshapen were separated from those which appeared normal. Normal eggs obtained by this method were measured and compared with eggs obtained from wood pores.

The suitability of wood shavings as an oviposition site was determined in a preliminary test using five groups of beetles. Each group, of 50 males and 50 females, was placed in a separate watch glass, prepared as described above, and left for 1 day. In all, wood shavings in 31 watch glasses were exposed to adult males and females.

Viability of Eggs and Incubation.—An undetermined number of males and females was placed on shavings in a watch glass, and on the following day 100 eggs that appeared normal were collected. These were transferred to numbered circles on glossy, black weighing paper in 10 separate 90–mm. petri dishes. The black paper permitted a clearer picture of visible changes taking place within the eggs. Daily observations were made until the larvae were completely free of the chorion. This procedure was replicated four times to determine the average incubation period of the viable eggs. Eggs which did not produce larvae free of the chorion were not considered viable. Observations were made also on the hatching of the eggs, and on the visible changes occurring in them during the incubation period.

Observation Cages.—Two types of cages were designed for observing the egg and the larval stages. Both types were filled with wood flour, made by pulverizing shavings to 50-mesh particles in a Wylie mill.

The two type A cages used (fig. 2) were made of wood strips, aluminum, and glass. An inner chamber, 2 mm. wide, was formed between two glass panes. Wood flour was poured into this chamber, moistened, and packed; and this process was repeated until the space was filled. The cages were then oven-dried at 120° C., after which the top of each was covered with aluminum foil. Several weeks later, channels about 1 mm. in diameter were made by forcing No. 2 dissecting pins into the flour where it adjoined a glass pane, and several eggs were inserted into these channels. Daily observations were made to determine viability, incubation period, and visible changes in the eggs.

The type B cages (fig. 3) were made by cementing glass strips, 75 x 4 mm., along the edges of a standard microscope slide. Wood flour was then thoroughly wet with water and spread on the slide, between the glass strips, until the space was completely filled. A second microscope slide was then placed over the two glass strips and the wood flour, so that the flour was entirely enclosed except at the two ends. Rubber bands around each cage held it together while it was oven-dried at120° C. for several days, after which the sides and one end were sealed with masking tape, and only one end was left open. To prevent the entry of unwanted beetles, all type B cages were kept in a pint jar with its wide mouth covered with a piece of muslin held in place by a rubber band.

Mechanical insertion of eggs here entailed the same procedure as with type A cages, and here also daily observations were made.

Type B cages were also used in studying oviposition habits. A small amount of wood flour was removed from the open end and a male and a female (or a female known to have copulated) were placed in the chamber thus formed. The open end was then sealed with a piece of wood and paraffin. Oviposition was observed several times in such chambers.

Records on the development of the young larvae in both types of cages were maintained from the time of their eclosion until they died or disappeared. When one had disappeared for several weeks, at least, with no reappearance on the surface of the wood flour, the cage was disassembled and the flour was carefully examined under 18x magnification for any signs of the larva.

Prepupa and Pupa.—No mention of a prepupa was found in the literature. However, while material collected by the following method was being examined, a larval specimen of peculiar shape (fig. 4) was found, and further examination revealed several other specimens of this sort. These were maintained in a petri dish, and the majority of them transformed to pupae.

Peeling off the thin outer shell present on heavily infested wood and examination of the area thus exposed proved a very slow and inadequate method for collecting pupae. The following technique, applicable either for pupae or for prepupae, proved far superior for obtaining these forms from infested wood maintained in the laboratory.

Two seed-sifting pans, with sieve openings of $\frac{3}{16}$ inch and $\frac{1}{12}$ inch, respectively, were placed over a seed-collecting pan, with the $\frac{3}{16}$-inch sifting pan above the $\frac{1}{12}$-inch pan. The outer shell, starting to disintegrate from the beetles' attack, was peeled from infested wood, and the disintegrating wood was shaken over the uppermost pan. Often the wood was almost completely powdered, and in such cases this material also was placed in the $\frac{3}{16}$-inch pan. Though wood fragments were caught in the two sifting pans, no pupae or prepupae were found in either of them. The material that had sifted through the $\frac{1}{12}$-inch opening was then sifted through a No. 20 U. S. Standard sieve, which did not permit the passage of pupae, prepupae, larger larvae, or wood fragments of corresponding size. Small amounts of the material retained by the No. 20 sieve were placed on glossy, black weighing paper where, under the light of a gooseneck lamp, prepupae and pupae were easily located and collected with an aspirator. No prepupae or pupae were found in the material that passed through this sieve.

For determining the duration of the prepupal period, circles of glossy, black weighing paper were placed in several petri dishes. These were divided into 10 compartments by wooden dowels, 2 mm. in diameter, which served as dividing walls, and prepupae were placed in the compartments. Daily observations were made on each prepupa until it pupated or died; visible changes were recorded, and prepupal molting was observed and recorded.

The duration of the pupal period was determined similarly, using individuals that had molted from prepupae. Additional information on pupal biology was obtained from such individuals, and from others collected by sifting infested wood.

Adults.—Counts and sex determinations were made of adults emerging from infested wood in the initial stock culture for approximately 8 months after the initial emergence.

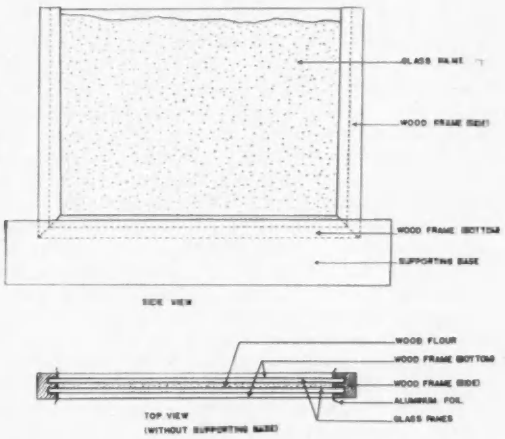

FIG. 2.—Type A cage used for observing the eggs and larvae of *Lyctus planicollis*.

In determining the total life span of newly emerged adults, a piece of heat-dried red-oak wood, approximately 1½ inches square by ¼ inch thick, was placed on filter paper in a petri dish. Such a dish, when closed, served as a cage for a single adult beetle whose time of eclosion was known within 1 day, and each beetle thus isolated was checked daily until it died. A part of the life span was thus spent under conditions not found in the beetles' normal environment.

Similar blocks of oak were used in determining the time interval between exit formation by an adult and its actual collection. These blocks were exposed to an undetermined number of adults, and the tests were started when adults began to emerge from them. Any exits then present were opened and the adults found in them were destroyed. Each block was then placed on wooden dowels which raised it 2 mm. above the filter paper in the petri dish and permitted free emergence of any adults that formed exits on the under surface of the block. Blocks were checked daily, and all new exits were circled with a pencil mark. A record was kept

of the time interval between formation of the exit and collection of the adult; after emergence of an adult, its exit was sealed with paraffin. Simultaneous formation of two exits on one block occurred very infrequently. If a second exit were formed before an adult was collected from an earlier one, both exits were opened and the adults were destroyed.

Beetles emerging from a stock culture of infested wood were used in determining the adult life span from actual collection until their death. Because beetles of undetermined age were found in cracks and crevices of the infested wood, the collections made during the first week were all discarded. Thereafter, the adults were collected daily for use in these tests. Blocks of uninfested wood, like those previously described, were placed in 80 petri dishes, and six adults, known to have emerged from the infested wood within the preceding 24 hours, were placed in each dish. Males only were placed in one group of 20 dishes, females only in a second group of 20 dishes, and three adults of each sex in the remaining 40 dishes. Daily observations were then made until all the adults were dead.

The theoretical time interval between the final ecdysis and the construction of an exit was calculated by subtracting from the average total adult life span the sum of the average time intervals from exit formation to actual collection and from collection until death.

Copulation and Oviposition.—Little information on these topics is found in the literature. Snyder (1916) and Christian (1940) discussed them briefly. Smith (1956b) reported a technique suitable for observation of oviposition and development of the egg.

The following techniques, developed during this study, yielded information on six phases of the copulation and oviposition habits. The investigations were initiated in an observation cage consisting of a glass ring, $\frac{3}{8}$ inch in height by $\frac{1}{8}$ inch in diameter, attached with paraffin to a filter-paper circle in the bottom of a petri dish. The beetles used were collected daily, each from a separate petri dish containing a red-oak block from which adults were emerging, as described above. Each beetle was known to have emerged from one exit in such a block, within a 1-day period, and all beetles emerging in this manner were assumed to be virgins. Males were identified by placing a small dot of white drawing ink on their elytra.

A male and a female were placed simultaneously in the glass ring, and the time interval until the first copulation was noted. Copulation was considered to be taking place when the male was positioned over the female, and a slight tilting of the petri dish revealed that the phallus of the male was inserted into the vulva of the female. All time intervals were measured with a stop watch. The copulation act was observed and described. Each pair was observed for 1 hour, and the number of copulations that occurred and the duration of each were noted. At the end of the observation period the beetles were removed from the ring with an aspirator.

In one-half of the pairs, following their removal from the ring, the female was separated from the male and was placed alone on a heat-dried, red-oak block, approximately $1\frac{1}{2}$ x 1 x $\frac{1}{4}$ inch, resting on a filter-paper circle in a petri dish. This block served as an oviposition site. Each female was transferred daily to a fresh wood block until her death, but none was transferred while ovipositing. All the wood blocks exposed to one female were cut from one billet.

The remaining pairs were not separated after their removal from the glass ring. The male and the female of each pair were placed together on a wood block like that described in the preceding paragraph, and were transferred daily to fresh blocks of wood, cut from the same billet, until the female died.

The wood blocks, after exposure to a female or to a male and a female, were placed separately in small jars with mouths covered with muslin held in place by a rubber band. In succeeding months checks were made at irregular intervals to determine whether females had deposited eggs in the blocks. A block was considered infested if visual examination revealed powder issuing from the block, or if adult beetles, one or more, were collected from the jar containing the block.

Oviposition Potential.—A modification of the "wood shavings technique" was developed to determine the number of eggs that a female might deposit in such a site. Petri dishes were prepared with five small glass rings (inside diameters $\frac{5}{8}$ to $\frac{3}{4}$ inch) fastened to the bottoms with paraffin. Shavings of air-dried red oak were obtained by the method described above, placed in water for about $\frac{1}{2}$ minute, then packed in the five glass rings. A cork, slightly smaller than the inside diameter of the ring, was placed on the shavings in each one, and a petri-dish cover was held tightly against the corks with rubber bands to prevent curling of the shavings while drying. The dishes were oven-dried at 120° C. for about 2 days, after which the rubber bands and corks were removed and the covered dishes placed in the laboratory.

Seven females, known to be virgins less than 1 day old, were placed, each with a male, in individual glass rings. A circular glass cover, slightly larger than the diameter of the ring, was placed over the top of each one and fastened to it with paraffin. All pairs, except the seventh, were transferred to shavings in a new ring at the end of each successive 4-day period during the experiment, which was continued for 20 days in some cases but was terminated after 16 days in others. The seventh pair was left for 6 days in the first ring, for 2 days in the second, then for

4 days in each of the succeeding rings. No transfers of any pairs were made while the ovipositor of the female was extended. After removal of the beetles from a ring, the shavings were carefully removed, one at a time, under continuous examination with 18x magnification, and the eggs were counted.

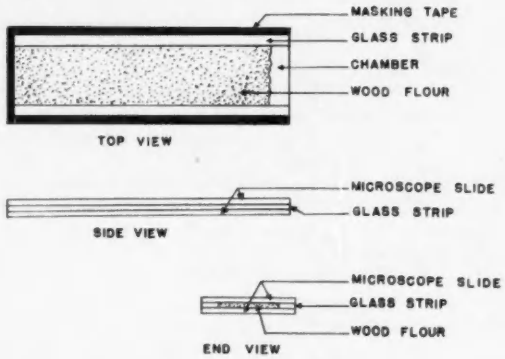

FIG. 3.—Type B cage used for observing oviposition, eggs, and larval development of *Lyctus planicollis*.

RESULTS

Eggs.—Average measurements of eggs deposited in wood shavings were: length of chorion, 0.984 mm.; diameter of chorion, 0.162 mm.; length of strand, 0.284 mm. These measurements confirm those given by Snyder (1916), Parkin (1934), and Smith (1956b) for eggs deposited in wood pores. Eggs deposited in wood shavings, then transferred to petri dishes, showed viability varying from 20 to 90 percent, with a mean of 64 percent, and the incubation period of 100 of the viable eggs anged from 4 to 12 days, with a mean of 8.17 days.

Eleven eggs were mechanically inserted into channels forced into the wood flour of the type A cage. Of these, eight did not produce larvae free of the chorion, two yielded larvae, eclosion date unknown, and one egg produced a larva free of the chorion in 8 days, which agrees closely with the average incubation period of eggs deposited in wood shavings. In type B cages, five eggs hatched out of six deposited by different females, with incubation period of 7 to 8 days (mean, 7.4 days), and seven hatched out of eight that were mechanically inserted in channels forced into the flour. The incubation period of these seven ranged from 7 to 11 days, with a mean of 9 days. The average incubation period for all 12 of the eggs that hatched in type B cages was 8.2 days, which is very close to the 8.17-day average for eggs kept in petri dishes.

Visible Embryonic Changes.—Within 1 day, a slight void became noticeable at the posterior end of the egg—the end opposite the strand. After 2 days, in eggs that had not become opaque and granular, the void was still visible. Within 3 days the egg was completely opaque, with a granular appearance. Faint differentiation of two or three areas, either opaque or translucent, was noticeable on the fourth day, and the granules were less evident. At 5 days the differentiation between embryo and yolk was becoming evident, and during the sixth day the two areas were completely differentiated. On the seventh day the larva, with lightly pigmented mouth parts, was visible inside the chorion. After 8 days the chorion was ruptured, and the larva was feeding on the yolk or had emerged from the egg shell.

Hatching.—Observations on the emergence of larvae from eggs deposited in wood shavings and in wood flour verified the posterior manner of hatching described by Snyder (1916). In one instance, however, the larva, after consuming the yolk, ruptured the anterior, or strand, end of the chorion and emerged there. Alston (1923) reported that this anterior type of hatching occurred in *Lyctus brunneus*.

Larval Period.—Observations on the length of time from hatching to cessation of larval activity and on the length of the inactive period were made on 7 of the 15 larvae which eclosed from eggs deposited by females or mechanically inserted in type A and type B observation cages. The other eight larvae tunneled into the wood flour after hatching and were not observed for several days; several of them did not emerge at all from the wood flour.

The seven larvae tunneled in the wood flour for 2 to 7 days after eclosion, and all of them passed pellets of excreta during this time. Not later than the seventh day, the larvae entered a period of inactivity which lasted for 2 to 3 days. Larval exuviae noted at the posterior tip of two larvae during this period of inactivity indicated that a molt occurred at this time, and in both cases the exuviae were found 1 day before activity was resumed. Possibly the other larvae also molted, became active, and in their movements destroyed or hid any cast exuviae during the 24 hours between daily checks.

Observations of larval activity after this molt became difficult because of frequent, irregular disappearances and reappearances of the larvae. Two disadvantages of type A and type B observation cages were noted. The thickness of the wood flour, even though only 1 mm. thick in a type B cage, allowed the larvae to burrow into the flour and become hidden; and all larvae living in the wood flour eventually died, of unknown causes. The length of the larval stage was not determined, but larvae were known to have remained alive in type A or type B cages for 42 days.

Prepupa.—A prepupal stage in *Lyctus planicollis* had not been noted before, though the shape of a prepupa is distinctly different from that of a mature larva (see fig. 4). Large larvae showed continual movement, except in a short time interval before molting, but little movement of

prepupae was discernible. Occasionally a faint, almost imperceptible, movement of the prepupal abdomen was noticed.

The length of 62 prepupae, collected by sifting infested wood, ranged from 2.75 mm. to 5.25 mm., with a mean of 3.92 mm. Tabulation of the data on 60 of these prepupae showed that 11 pupated on the second day after collection, 15 on the third day, 10 on the fourth day, and 2 on the fifth day, while 22 of the 60 did not molt to pupae. This gave a prepupal mortality of 36.7 percent. Little morphological change during the prepupal stage was visible. During the last day in this stage, the pigmented eye facets of the pupa forming under the prepupal skin were usually discernible.

Table 1.—Calculation of the time lapse between eclosion of adults and construction of an exit by males and females of *Lyctus planicollis*.

Phase of adult life	Mean duration (days)	
	Male	Female
A. Total span (adult eclosion to death)	33.1	35.1
B. Exit formation to emergence of adult	4.9	2.2
C. Emergence of adult to death[a]	14.0	14.7
B+C.	18.9	16.9
A–(B+C). Adult eclosion to formation of exit	14.2	18.2

[a]The means for males and females kept separate from one another were used because the means of A were determined on this basis.

Molting of a prepupa to a pupa began with the prepupa swelling until the integument was tightly stretched. A small slit appeared transversely over the pronotum. This slowly enlarged and the pupal pronotum gradually emerged through it. After the pronotum was completely exposed, the prepupal integument split on each side of the body to the laterosternal juncture of head and thorax. The vertex of the head was then gradually freed of its exuvial covering, with the posterior portion of the vertex being exposed first. After the pupal head was freed, a slit formed laterally along the abdominal wall, and by irregular movements the exuvia was freed from the remainder of the body.

Pupa.—The length of 135 pupae ranged from 2.75 to 5.75 mm., with a mean of 4.21 mm. Daily observations were made on the 38 pupae which molted from prepupae. Twelve of these died, giving a mortality of 31.6 percent. For the other 26 the average duration of the pupal period was 8.12 days, with 3 individuals transforming to adults in 7 days, 17 in 8 days, and 6 in 9 days. The visible, day-by-day changes during pupal development are summarized in the following outline:

Table 2.

Frequency and duration of copulations by 20 pairs of adult *Lyctus planicollis* in a 1-hour period.

Pair number	Number of copulations	Duration of copulations (minutes)							
		1st	2nd	3rd	4th	5th	6th	7th	8th
1	6	3.0	2.2	0.7	0.2	0.5	0.3	—	—
2	3	2.4	0.3	0.6	—	—	—	—	—
3	1	1.3	—	—	—	—	—	—	—
4	3	3.0	1.2	0.3	—	—	—	—	—
5	4	1.8	1.6	1.1	0.3	—	—	—	—
6	3	3.3	0.5	0.3	—	—	—	—	—
7	7	1.4	2.5	2.1	0.5	1.0	0.4	0.7	—
8	5	1.5	0.5	1.0	0.7	1.0	—	—	—
9	5	2.9	0.4	0.4	0.5	0.2	—	—	—
10	4	2.3	0.5	0.4	0.7	—	—	—	—
11	4	2.7	0.3	0.7	0.4	—	—	—	—
12	2	2.5	1.0	—	—	—	—	—	—
13	3	1.1	0.5	0.7	—	—	—	—	—
14	4	0.8	0.2	1.1	0.4	—	—	—	—
15	6	2.1	1.4	0.9	0.3	0.4	0.3	—	—
16	8	4.2	0.6	1.0	0.7	0.4	0.5	0.8	0.2
17	4	0.9	0.5	0.5	0.3	—	—	—	—
18	8	4.7	0.6	0.4	0.4	0.2	0.7	0.4	0.3
19	7	1.8	0.6	0.5	0.2	0.2	0.3	0.3	—
20	3	2.9	0.5	0.3	—	—	—	—	—
Averages	4.55	2.4	0.8	0.7	0.5	0.5	0.4	0.5	0.3
Pairs copulating		20	19	18	13	8	6	5	2

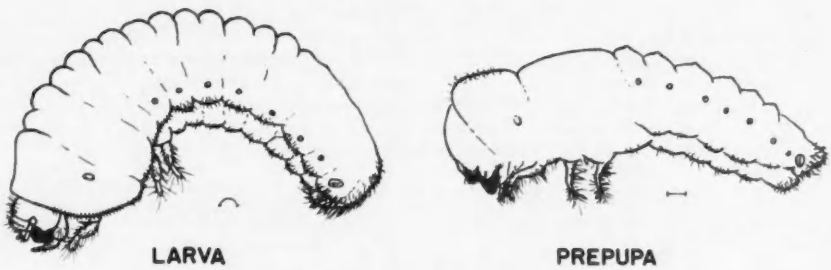

FIG. 4.—Larva and prepupa of *Lyctus planicollis*.

DAY
0 Prepupa transformed to pupa within the last 24 hours; pupa white, with the centers of many eye facets pigmented.
1–3 Gradual darkening and enlarging of the pigmented centers of the eye facets.
4 Eye facets completely pigmented; faint traces of pigmentation present at bases of mandibles.
5 Mandibles pigmented.
6 Head and thorax light-brownish; tarsal claws and tibial spurs pigmented and moving under their pupal covering; pigmented articulation joints visible between coxa and trochanter, and between femur and tibia of all legs.
7 Frontal area of head and pronotum lightly sclerotized; ventral metathoracic segment deeply pigmented; antennae and legs sclerotized; posterior fringe of last abdominal sternite lightly pigmented; dark gray areas on center or dorsomeso- and dorsometathoracic segments; tarsi of all legs moving, though the legs remain in their pupal position; wing raised slightly from normal pupal position.
8 Adult emerged.

Adults.—The size range of adults was: males, 2.5 to 5.5 mm. (mean, 3.51 mm.); females, 2.75 to 5.25 mm. (mean, 3.67 mm.). The sex ratio in a stock culture was 1,723 males (50.56 percent) to 1,685 females (49.44 percent).

Early observations indicated that the total adult life span was divisible into three phases: from adult eclosion to appearance of exits in the wood, from the appearance of such exits to the actual emergence of the adult from the wood, and the observed life span after emergence from the wood.

Adults collected upon molting from pupae lived, in some instances, more than 1½ months. The total life span of 19 males ranged from 21 to 44 days, with a mean of 33.1 days, while that of 26 females ranged from 11 to 58 days, with a mean of 35.1 days.

The time interval between formation of an exit and actual collection of the adults (27 males and 39 females) varied within and between the sexes. In eight cases adults were collected on the same day when the exit was formed. The majority of the males were collected from the second through the fourth day, while the largest number of females was collected in the first 3 days after exit formation. All females were collected within 8 days, but four males were collected 14 days after they formed exits. The average number of days between exit formation and collection was 4.9 for males, 2.2 for females.

The observed life span of 480 adult beetles after emerging from wood varied between 2 and 42 days. The mean life span was 14 days for males kept apart from females, 13.8 days for males associated with females, 14.7 days for females isolated from males, and 13.1 days for females associated with males.

The theoretical duration of the interval between adult emergence from the pupa and constructions of an exit was calculated from average total duration of the adult stage, the mean number of days between exit formation and collection of the adult, and the mean number of days from adult emergence from the wood until death (table 1). The calculated mean time interval between ecdysis from the pupa to construction of an exit was 14.2 days for males, 18.2 days for females.

The interval between introduction of males and females and their mating varied, in 20 pairs, from 0.8 to 27.5 minutes, with a mean of 8.1 minutes. All of the pairs but one mated in less than 18 minutes. After a male and a female were placed in a glass ring, the male crawled on the dorsal part of the abdomen of the female, and copulation was begun. Usually both beetles remained quiet for a short time, then the female started crawling and apparently attempted to dislodge the male. The male usually retained its position by moving its legs rapidly over the lateral areas of the female's abdomen, but eventually was dislodged and copulation ceased.

Table 2 gives the duration of each copulation by 20 pairs of adults. In all tests but one, the first copulation was of much longer duration than those which followed, and in the majority of the tests each successive copulation by a pair was shorter than the preceding one. The number of copulations per hour for the 20 pairs ranged from 1 to 8, with a mean of 4.55 per pair.

Females began depositing eggs shortly after mating. There was no difference in the interval from copulation to oviposition between females isolated from the males after a 1-hour mating period and females allowed to remain with males

throughout their adult life, and there was little difference between these groups in the length of time over which females deposited eggs. Eighteen females deposited viable eggs within 1 day after mating, and the other two did so within 3 days, giving an average of 1.2 days. Females that remained in constant association with males deposited viable eggs for 1 to 15 days, with a mean of 4.7 days, while females separated from males did so for 1 to 8 days, with a mean of 4.3 days. In numerous cases oviposition was stopped for a day or two, then resumed and continued for several days. Females lived from 5 to 15 days after deposition of the last viable egg.

Table 3.—Number of eggs deposited in successive 4-day periods by females of *Lyctus planicollis*.

Female	Days 1–4	5–8	9–12	13–16	17–20[a]
A	31	18	13	1	—
B	46	0	0	0	—
C	66	49	7	0	—
D	13	2	3	0	—
E	18	14	3	0	—
F	15	7	3	0	—
Mean	31.5	15.0	4.0	0.2	0

[a]All females were dead at the end of this period.

In six tests made with one female per petri dish, the average rate of oviposition was highest during the first 4 days after mating, declined by about one-half during the next 4 days, and reached zero for all but one of the females at the end of the third 4-day period (table 3). The total number of eggs deposited and collected ranged from 18 to 122 per female, with a mean of 51.4. Of the eggs checked, 91.9 percent appeared normal and conformed to the description given by Snyder (1916). The remaining 8.1 percent were collapsed, shriveled, or otherwise misshapen when collected.

Females placed on wood shavings deposited large numbers of eggs daily (table 4). In five watch glasses, with 50 females in each, the total number of eggs collected in 1 day ranged from 256 to 461 per dish (mean, 369), corresponding to an average of 7.2 eggs per female per day. Of these eggs, 93.1 percent were normal. The eggs which were misshapen did not hatch.

Oviposition in the wood flour of a type B cage was observed on July 2, 1957. Immediately after a male and a female were placed in the small cavity in the cage, the female moved to the wood flour and appeared to chew on the wood fragments, possibly testing the suitability of the wood for egg-laying. Such testing of the wood for starch was reported by Christian (1941). Chewing of the fragments soon was stopped. The ovipositor was then extruded and used for rapid exploratory movements, seemingly at random, in the vacant spaces between wood fragments lying against the glass wall of the cage. This probing continued for approximately 4½ minutes, during which the ovipositor was drawn back into the abdomen several times, then immediately reexserted, up to a maximum of 1¾ mm. from the posterior tip of the abdomen. The female then became quiet for a few seconds, with the ovipositor fully extended. After this brief inactive period she began a pumping movement with the whole body which lasted approximately 1½ minutes. Near the end of this pumping period a light, translucent egg was seen to pass down the length of the ovipositor and emerge at its tip. The strand of the egg left the ovipositor last. Approximately 6 minutes elapsed during the exploratory, probing, pumping, and egg-laying movements, and during this time movement of the cage did not stop any of these actions. Probing with the ovipositor continued after the egg was laid.

Table 4.—Number of eggs deposited in wood shavings in 1 day by 50 females of *Lyctus planicollis*.

Dish	Total eggs	Normal	Misshapen
		%	%
A	391	91.6	8.4
B	256	95.0	5.0
C	390	91.0	9.0
D	461	93.0	7.0
E	348	95.0	5.0
Total	1,846		
Mean	369	93.1	6.9

In turning the cage a sharp, unintentional tap was made on one of its walls. The female immediately retracted the ovipositor into the body, then, after remaining quiet for a few seconds, extended it again and commenced short, infrequent probings into the spaces in the wood flour. However, no further egg deposition occurred in the next 30 minutes.

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ANGELOTHROMBIUM PANDORAE N. G., N. SP. (ACARI, TROMBIDIIDAE), AND NOTES ON THE BIOLOGY OF THE GIANT RED VELVET MITES[1]

IRWIN M. NEWELL[2] AND LLOYD TEVIS, JR.[3]

ABSTRACT

Both larval and adult stages of this new genus and species are described, rearing having permitted their correlation. As in the related genus *Dinothrombium*, larvae are parasites on grasshoppers, and the adults are predators on termites. As far as is presently known, the new species is largely confined to the fine sands of the Coachella Valley of southern California.

The giant red velvet mites are the largest and most colorful of the Acari. They are especially common in desert and semi-desert areas, but are found also in some of the more humid parts of the tropics and warm temperate zones. In some places they emerge in such great abundance after heavy rains that they literally cover the ground and can be counted by the thousands. Because of their large size (up to 13,000μ in the African *Dinothrombium tinctorium* (Linn.) 1767) and brilliant crimson or crimson-and-white markings they attract considerable attention and are often well known by local inhabitants in the parts of the world where they occur.

Robert Beer of the University of Kansas has told the writers (in lit.) of an exceptional eruption of what must have been one or more species of *Dinothrombium*. The emergence was sighted from the air at an altitude of approximately 1,500 ft. near the town of Picacho, Arizona, about 48 miles northwest of Tucson. At first it was thought that it might be an unusual bloom of some desert lichen, but an inspection of the area from the ground revealed that it was in reality a heavy emergence of giant red velvet mites. An estimated 40 or 50 mites were found in each 4-inch square (16 square inches). This very heavy emergence was observed over an area of approximately 2 acres, beyond which the mites decreased in numbers. Very few mites were found outside of an area of approximately 5 acres. The population was not actually sampled, but if we accept these figures at their face value, the number of mites involved was of the order of 3 to 5 million. The eruption of the mites occurred almost immediately after a heavy but brief summer rainstorm, on August 3, 1943. The storm was of the type so characteristic of the summer rainy season in this part of the country, with a column of rain progressing across the desert. These storms are ordinarily of small diameter, but the rainfall within them is intense.

A number of species of giant red velvet mites are found in western North America. Thor and Willmann (1947, pp. 445–446) listed five species from the United States and Mexico:

Dinothrombium colhuanum (Vitzthum) 1933, Mexico (Guerrero).
Dinothrombium magnificum (LeConte) 1852, Texas and New Mexico.
Dinothrombium mexicanum (Stoll) 1893, Mexico (Presidio).
Dinothrombium superbum (Banks) 1910, Arizona (Tucson).
Dinothrombium dugesii (Trouessart) 1894, southeastern Mexico.

The first of these is a relatively small form, gravid females measuring only 2500μ in length. It may not be a *Dinothrombium*. In addition, Vitzthum (1933, page 233) listed *Dinothrombium tinctorium* as occurring in Mexico, but no further details were given. The writers have found no verification of this record elsewhere in the literature, and the record is probably erroneous. Despite the large number of species (25–30) which have been named and ascribed to this genus, from all parts of the world, little appears to be known of the biology of these forms.

With a view to learning something of their biology, the authors undertook a study of a large red mite of the general facies of the genus *Dinothrombium* which occurs in the Coachella Valley of southern California. The biological investigations are still under way, but a number of important facts have been established, including the site of egg deposition, the larval host and the food habits of the adult. These have led in turn to the discovery of the larvae of several species of *Dinothrombium*, the hosts of these larvae, and the habits of the adults. As a consequence of detailed morphological studies, it is now clear that the Coachella Valley mite is sufficiently distinct from species of *Dinothrombium* that it must be placed in a different genus.

The precise status of *Dinothrombium* Oudemans 1910 is uncertain, and clarification must await a restudy of *Dinothrombium tinctorium* (L.) 1767. On the basis of what we now know, however, the species presently listed under this genus will probably prove to belong in a number of genera. Feider (1952) presented the intriguing view that *Paratrombium* Bruyant 1910 (=*Parathrombium* Auct.) and *Dinothrombium* are one and the same

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genus. However, Feider's views were apparently based only on his discovery that a mite which he identified as *Dinothrombium insulare* Berlese 1910 var. *divisipilli* Feider 1948 was, on the basis of rearing studies, nothing other than a *Paratrombium*. There is no question that the larva described by Feider in his 1952 paper is the larva of a *Paratrombium*, but even if Feider were correct in identifying his variety with *Dinothrombium insulare* Berlese 1910, which is improbable, this does not affect the final status of *Dinothrombium*. This can be determined only by a restudy of the type species of the latter genus. So far as can be judged from the study of our North American *Dinothrombium* or *Dinothrombium*-like species there is no possibility that *Dinothrombium tinctorium* will ever be shown to be congeneric with *Paratrombium egregium* Bruyant 1910, the genotype of *Paratrombium*. Feider's views on the identity of *Dinothrombium* and *Paratrombium* must, therefore, be abandoned, and *Dinothrombium* must be recognized as a valid genus.

The biology of the giant red velvet mites of North America has proved to be of great interest. The larvae are parasites of many species of grasshoppers, in which respect they resemble the genus *Eutrombidium* Verdun 1909. Morphologically, however, they are very different, and their place of attachment to the host is also markedly different from that of the larvae of species of *Eutrombidium*. The adults are equally interesting, for they appear to be virtually specific predators on subterranean termites. Studies of the adults are hampered by the fact that they spend no more than a few hours of each year above the surface of the ground; the rest of the time they are buried from sight.

According to Edmund C. Jaeger (1957, p. 82), a leading authority on North American deserts, the giant red velvet mites in northern Mexico are called "angelitos"—little angels. This colorful folk name is undoubtedly applied to a number of species, including, perhaps, the one described below. We are memorializing it in the generic name of the species described here. The specific name, *A. pandorae*, is based on the Pandora of mythology, in recognition of the way in which research on this species—the first of the giant red velvet mites to be identified in both larval and adult stage, and the first one in which the larval and adult hosts have been determined—has raised the lid on knowledge of the biology of the genus *Dinothrombium*.

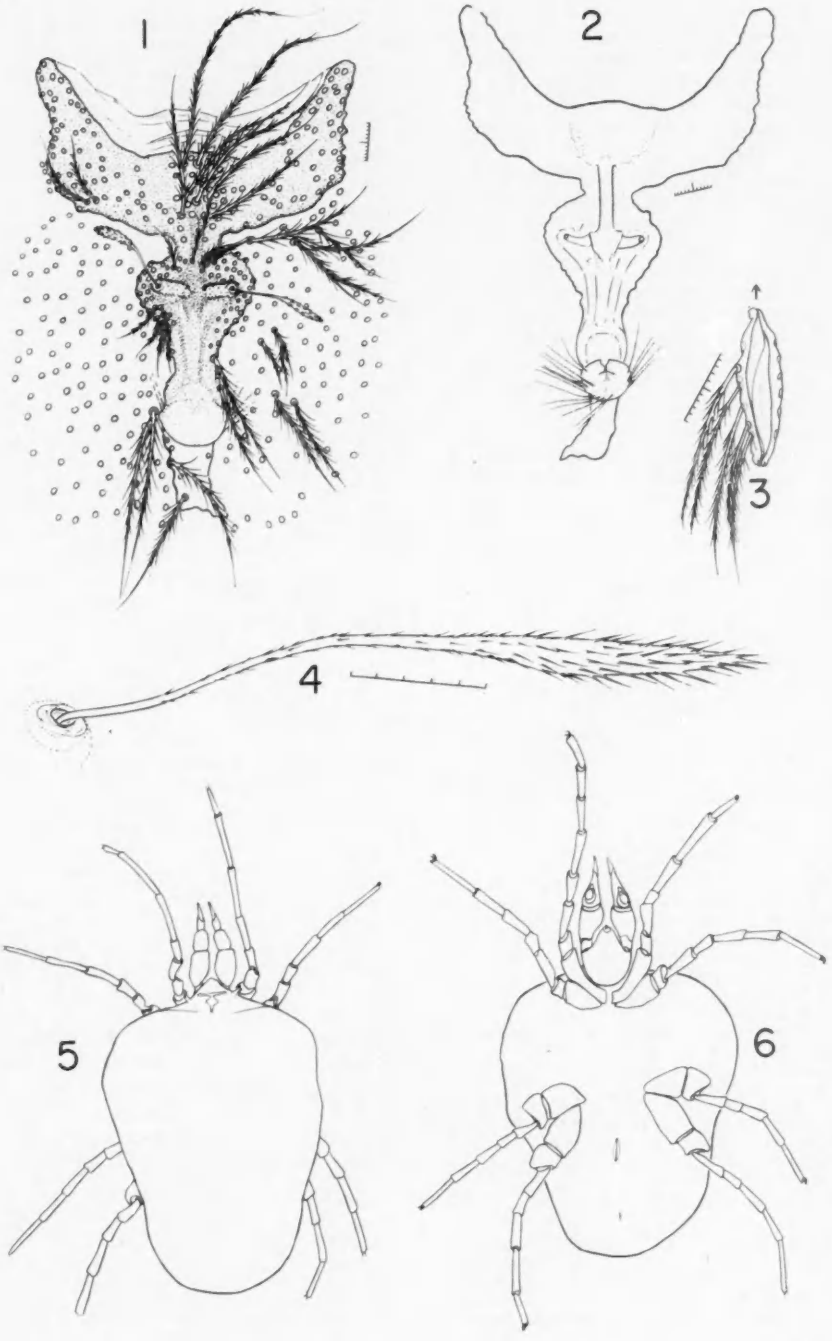
The present work was supported by a research grant (NSF–G 1833) from the National Science Foundation to the University of California, Riverside. The drawings were prepared by Mari Riess. In the figures, the scales provided are marked off in 10-micron units or in 100-micron units. The 100-micron scales are drawn with a double base line.

Angelothrombium, new genus

ADULT.—For the present, the characteristics of the genus must necessarily be those of the type species. Very similar to adults of the genus *Dinothrombium*, and indistinguishable from these by gross details. Body large, up to 7800μ, exclusive of gnathosoma and legs. Color brilliant red. Scutum with a broad transverse plate at the anterior end, separated from the portion bearing the areolae by a deep constriction (fig. 1). Sensilla with distal portion clavate-fusiform. Scutum with a posterior caudiform projection which is not pigmented and is therefore difficult to make out except in dissected material. At the anterior end of the caudiform projection is a circular portion with a deep central concavity (figs. 8, 9, 10), and numerous radiating filamentous apodemes. Setae in any one portion of body of same type, not differentiated into major and minor setae. Setae arising from minute ringlike sclerites which are not borne on elevated papillae. Coxal ring I not completely closed dorsally; with a heavily sclerotized prong which partially surrounds the insertion of the cylindrical ocular plate. Coxal ring II open dorsally. Supracoxal seta present on I. Genital and paragenital sclerites well developed, bearing numerous peripectinate setae; three pairs of genital acetabula. Tarsus of chelicera minutely denticulate along dorsal margin. Gnathosoma with a supracoxal seta in the synarthrodial membrane between the base of the gnathosoma and the trochanter; a number of pectinate setae also present here. Odontus massive in form, not a simple spiniform seta at the end of the tibia as in most genera of smaller Trombidiidae, but a heavy cap covering the dorsal and ventral surfaces of the pars distalis tibiae. Tarsus of palp with about five solenidia posteriorly and dorsally in the distal one-fifth of the segment. Tibia with no ctenidium. Tarsus I with two groups of slender, hemipectinate setae just ventral to the insertion of the tarsal claws. Setae of tibia and tarsus I of more or less uniform height and slope, eupathidia not projecting above the

EXPLANATION OF PLATE I

FIGS. 1–6.—*Angelothrombium pandorae*, new species, adult. FIG. 1.—Scutum, dissected from holotype male, cauda slightly atypical. FIG. 2.—Scutum, ventral view, showing crista metopica, subareolar pits and apodemes arising from callosity at anterior end of cauda. FIG. 3.—Anal sclerites, male. FIG. 4.—Sensillum and areola, right side, male. FIG. 5.—Dorsum, female, all setae omitted. FIG. 6.—Venter, female.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general level of the setae of this segment. Both tibia and tarsus I with numerous eupathidia on ventral surface as well as on dorsal surface. Trochanters III and IV very powerful, subspherical, their form evidently associated with the burrowing habits of the mites. Anus with a pair of well defined but narrow sclerites bearing a single row of setae.

LARVA.—Scutum with four pairs of setae including one pair of sensilla and one pair of prosensilla,[4] the latter not resembling the sensilla in form.

Posterolateral setae of scutum lying between the sensilla, far removed from the posterolateral angles of the scutum. Postscutum with only a single pair of setae, at least in the type species. Other dorsal setae borne on individual setigerous sclerites. Ventral coxal setae numbering (2–2–1); a single pair of intercoxal setae. Urstigma present but very small. Anal plates lacking. *Lassenia*-organ absent. Palpi four-segmented, trochanter absent; femur lacking setae, odontus of tibia bifurcate. Palpal tarsus with no typical eupathidiform setae, and no typical solenidion; six normal setae of various kinds present, plus two very minute terminal or subterminal setae in the type species. Rostrum with only the protorostral and tritorostral setae. Basifemur and telofemur of all legs fused, legs with only five free segments beyond the coxa. Solenidial formula of patella (2–2–2), of tibia, (2–2–0), and of tarsus (1–1–0). Vestigial setae present on patella I and II and tibia I, famulus on tarsi I and II; companion setae absent. All tarsi with three claws each, but with posterior claw of III reduced to a short, nearly straight rudiment.

TYPE SPECIES: *Angelothrombium pandorae*, new species.

[4]From studies on the Johnstonianidae it is evident that the anterior median setae of the scutum either may be a true second pair of sensilla (as in certain Johnstonianidae and most Erythraeidae), or may resemble the other setae of the scutum in form. In either case they are clearly the homologues of the anterior sensilla, and the term *prosensilla* is therefore deemed appropriate to designate these setae.

One further point of setal terminology should be made. Newell (1957, page 407), in a table of equivalent terms, listed "microfemorala, microgenuala, and microtibiala (in part)" as equivalents of solenidion$_3$. Also, "microtibiala (in part)" were listed as equivalent to solenidion$_4$. These equivalents were incorrect and should be changed to read: solenidion$_3$=femorala, genuala, tibiala (in part), and solenidion$_4$=tibiala (in part).

Angelothrombium pandorae, new species

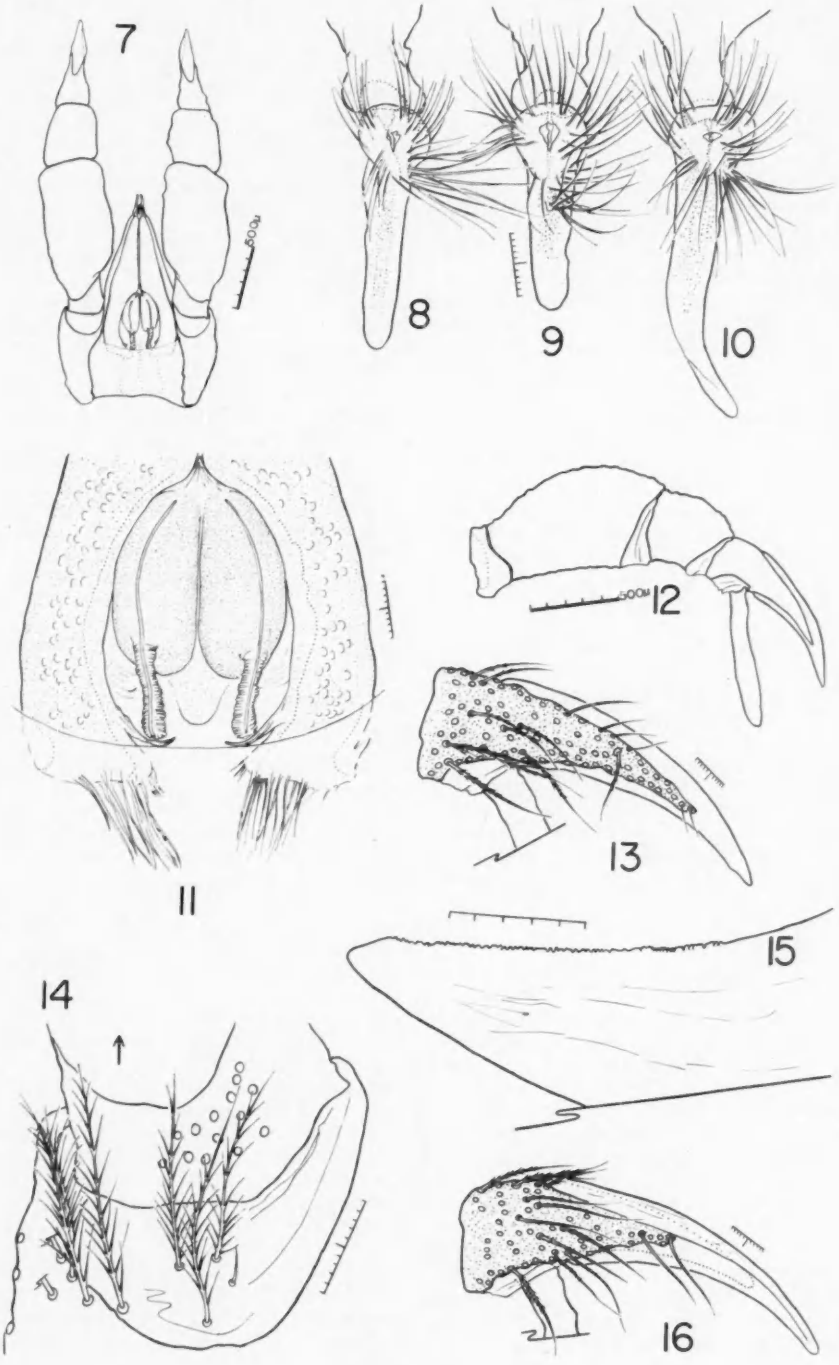
Of the 235 living specimens captured on the surface of the sand, or dug from the sand, the 11 largest measured 7,400μ–7,800μ to the anterior end of the idiosoma and averaged 7,560μ. These were not identified to sex. The 11 smallest individuals (stage and sex unknown) measured 4,000μ–5,200μ and averaged 4,860μ. The average length of all 235 mites was 6,470μ.

MALE.—Scutum of holotype male (fig. 1) with well developed anterolateral lobes delimited from the posterior portion of the scutum by a marked constriction between 0.23 and 0.30. Sensilla (fig. 4) with distal portion fusiform-clavate, pectinate. The alveoli of the sensilla are located at the lateral ends of a transverse ridge, ventral to which is a pair of deep transverse internal pits. The crista metopica is a short internal keel lying between 0.17 and 0.43. Just in front of the anterior end of the crista metopica is a central area containing about 30 of the longest setae on the scutum. At 0.68–0.82 is a large internal callosity to which the posterior apodemes of the scutum are attached. Behind this, the scutum is produced into a caudal portion, which is fairly well differentiated from the remainder of the scutum (the cauda is atypical in the holotype). Along the anterior margin of the scutum, the cuticle of the membranous area is considerably thickened and slightly darker than the remainder of the membranous cuticle, and is marked by rather prominent transverse rugae. Virtually all portions of the scutum bear setae, although they are more numerous in the area immediately surrounding the sensilla, in the area anterior to the crista metopica, and in the anterolateral lobes. Ocular plates stalked, about 280μ long, bicorneate. Dorsal propodosomal setae shorter and more delicate than those farther back on the body, arising from very minute ring-like sclerites imbedded in the membranous cuticle. Shaft uniformly tapering, and with a large number of delicate barbs, those near the base of the shaft longer than those near the apex of the seta. Subcuticular reticulum well developed. Three pairs of genital acetabula. Penis relatively short, conical in form. Anal sclerites narrow, but heavily sclerotized, bearing seven to eight setae each.

Tip of rostrum not reaching to end of femur of palp. Base of gnathosoma open wide dorsally

EXPLANATION OF PLATE II

FIGS. 7–16.—*Angelothrombium pandorae*, new species, adult. FIG. 7.—Gnathosoma, dorsal view, male. FIGS. 8, 9.—Cauda, male, ventral view, two specimens. FIG. 10.—Cauda, female, ventral view. FIG. 11.—Tracheal openings and peritreme, dorsal view. FIG. 12.—Outline drawing of palp, male, posterior aspect. FIG. 13.—Palpal tibia, posterior, male. FIG. 14.—Membranous cuticle at base of left palp, male, showing normal setae and supracoxal seta in the membranous area. FIG. 15.—Distidorsal margin, chelicera of male. FIG. 16.—Tibia, palp, anterior aspect.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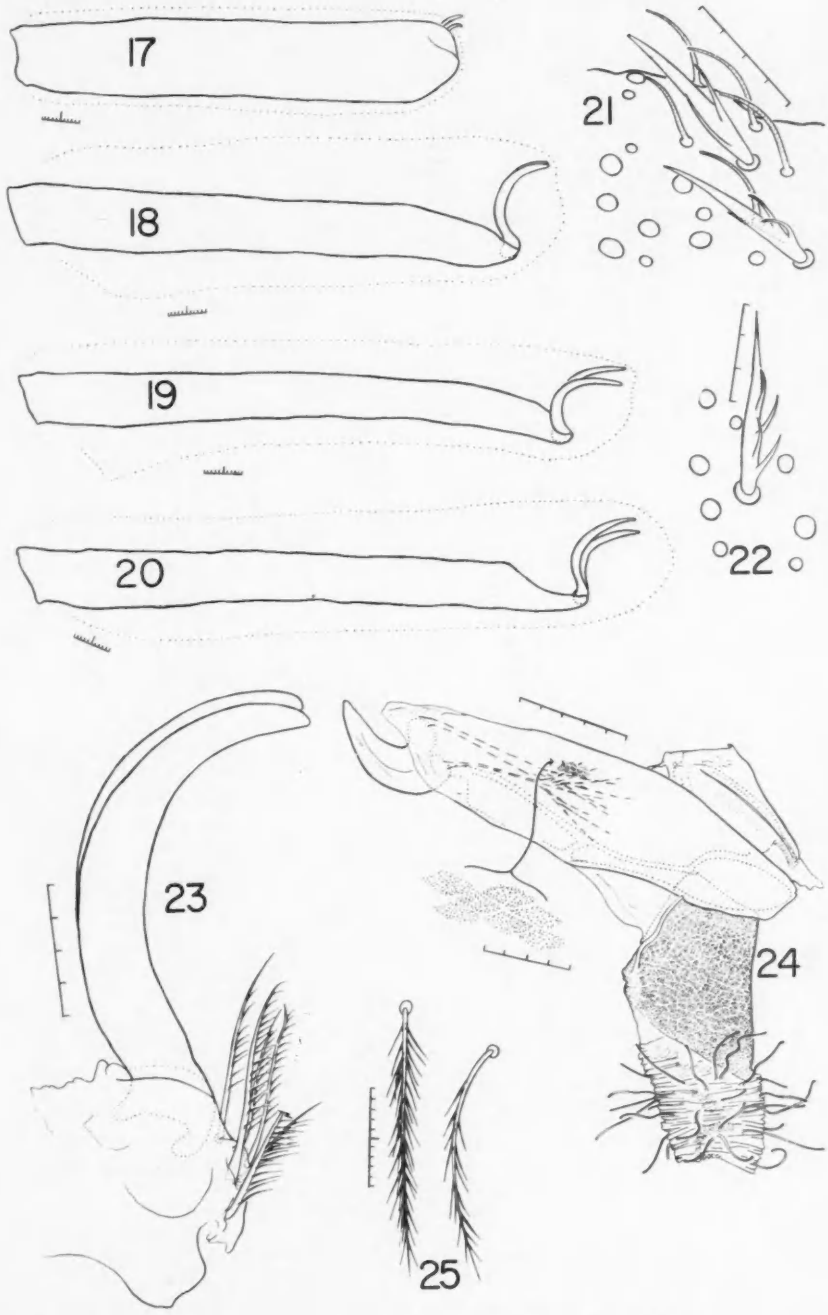
(fig. 7). Openings of tracheal system as shown in figures 7 and 8. Chelicerae (figs. 24 and 15) with distal half of tarsus minutely serrate along upper edge. Synarthrodial membrane at base of trochanter with a number of peripectinate setae plus the simple supracoxal seta (fig. 14). Length of segments of palpi rather variable even in the right and left palpi of individual mites, as shown in accompanying table, which gives the measurements for both palpi of each mite. In this table, the length of the tibia (LTi) is measured from the base of the tibia to the extreme tip of the tibia minus the odontus. This is done to minimize one possible source of variation in the measurement, namely variations in the length of the odontus due to wear. The pars distalis tibiae is that portion of the tibia beyond the insertion of the tarsus. The ventral length of the pars distalis tibiae is measured from the anterior margin of the opening in which the tarsus is inserted (tarsal foramen) to the tip of the tibia, exclusive of the odontus. The measurement is included here because the relative length of this portion of the tibia is known to have some specific value in other genera. The odontus is of unusual form in this genus, in keeping with its function as an important digging tool. It is quite wide as seen in dorsal or ventral view (fig. 7) and completely covers the dorsal and ventral surfaces of the distal half of the tibia. The anterior edge of the odontus is produced into a knife-like ridge (figs. 7, 16) The punctate setigerous portion of the tibia extends considerably farther on the posterior surface than it does on the anterior surface (compare figs. 13 and 16). The proximal setae on the tibia are peripectinate, but the more distal ones are smooth. Tarsus of palp usually with about five solenidia posteriorly and dorsally beyond 0.83. Tip of tarsus also with 10 to 15 large eupathidia, and numerous barbed setae

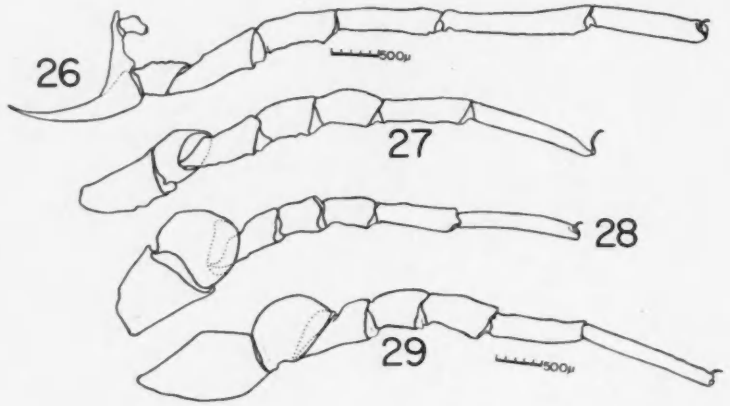
Supracoxal seta of coxa I similar in form to that of the gnathosoma, 41μ long in the specimen measured. Coxal ring nearly complete dorsally, and enclosing the base of the cylindrical ocular plate. Tarsus I considerably shorter than tibia I. Tarsus I with two groups of seven or eight unusually long hemipectinate setae ventral to the insertion of the tarsal claws. The insertions of the setae are hidden in the dense vestiture of setae. These are undoubtedly homologous with the single pair of heavy aliform setae (false empodium) at the tip of tarsus I of *Allothrombium*, but differ considerably in form. It is possible that the aliform setae (Grandjean 1943) of *Allothrombium* are composite setae, or, alternatively, that in *Allothrombium* only one of the group of homologues in *Angelothrombium* has become greatly enlarged. The normal setae along the dorsal surface of tibia and tarsus I are considerably different from those on the corresponding segments of the other legs. They are smooth, broad at the base, taper quickly to a sharp point, and bear from one to five stout barbs (figs. 21, 22). The normal setae along the ventral surface of these same segments have somewhat the same form, but are not so heavy. Measurements of tibia and tarsus are shown in the table below. There is considerable variation in the length of these, even in the six specimens measured; the longest tarsus I measured 43% longer than the shortest. The shortest tarsi were on the male with the shortest body length and the smallest palpi, although the scutum of this mite was not especially smaller than the scutum of the other specimens. Pars medialis coxae not developed. Coxa II considerably thicker (in the antero-posterior direction) than coxa I. Trochanter II somewhat more spherical than trochanter I. Trochanters III and IV greatly swollen and subspherical, especially trochanter III. Tarsi II–IV very slender, tapering perceptibly in distal 0.2; claws slender, smooth, erect. Genital and paragenital sclerites well developed, bearing numerous setae which are smaller than those of the surrounding body cuticle, but of similar form (fig. 25).

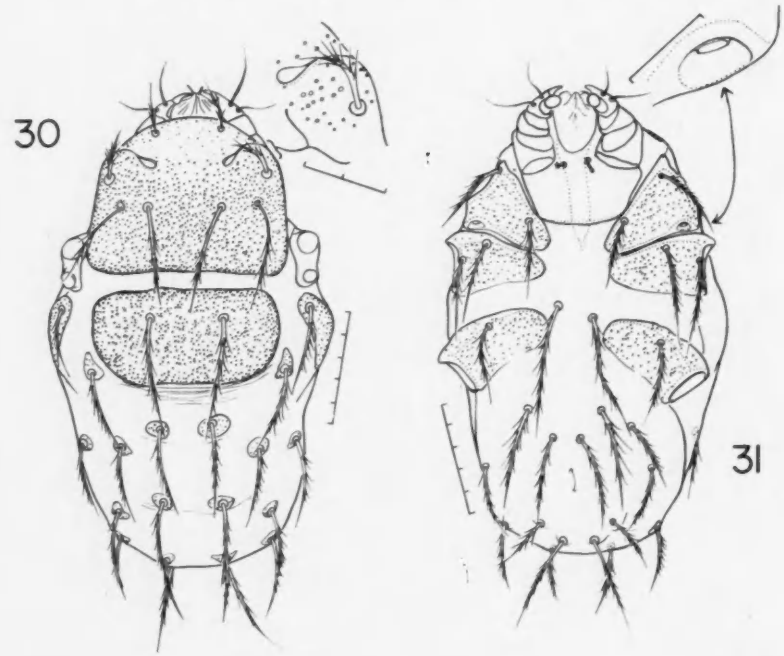
FEMALE.—The female is similar to the male in most respects except for the internal genitalia and the tibia and tarsus of leg I. Generally, the female is somewhat smaller than the male at the time courting pairs are found on the surface of the sand. This relationship may be reversed by the time the females have become gravid, but data are not now available on body size of gravid females. A few apparent sexual differences are evident in the table below. There is no significant sexual difference in the length of the femur, patella, tibia or tarsus of the palp. Where any discrepancies are noticeable, the average values for the female are very slightly higher. The proportions of the segments of the palp are identical in the two sexes on the basis of the figures presently available. Turning to the tarsus and tibia of leg I, however, a different picture is seen. The average length of the twelve tarsi I of the males measured was 1211μ, compared with 966μ for the six tarsi I measured in the females. Tibia I is also longer in the male (1514μ compared with 1213μ), but the relative proportions of tarsus I and tibia I within either sex are identical (0.80 in the cases available). Tarsus I is essentially the same height in the two sexes (215μ in the males, 212μ in the females measured). Consequently, tarsus I of the male is relatively more slender (5.63x as long as high), than in the female (4.55). There was no overlapping in this characteristic in the specimens measured, the ranges being 5.23–6.02 for the six males, and 4.00–4.82 for the four females.

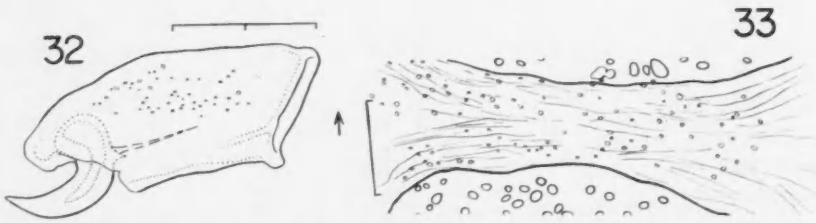
LARVA.—Idiosoma (fig. 30) very small, 188μ–200μ long, 120μ–131μ wide, length/width 1.50–1.63 (average of 10 unengorged specimens: 197μ long, 124μ wide, length/width 1.58). Scu-



FIGS. 17–25.—*Angelothrombium pandorae*, new species, male. FIGS. 17–20.—Tarsi I–IV, respectively. Dotted lines show extent of setal vestiture. FIG. 21.—Solenidia and normal setae of tarsus I. FIG. 22.—Normal seta with four barbs, tarsus I. FIG. 23.—Tip of tarsus I, dissected, showing claws and specialized setae below insertion of claws. FIG. 24.—Chelicera and main tracheal trunk. FIG. 25.—Ventral hysterosomal seta (left), and seta of genital sclerite (right).







FIGS. 26–29.—*Angelothrombium pandorae*, new species, male, legs I–IV. FIGS. 30–33.—*Angelothrombium pandorae*, new species, larva. FIG. 30.—Dorsum. FIG. 31.—Venter. FIG. 32.—Chelicera. FIG. 33.—Cuticle between coxa II and III.

Table 1.—Measurements of tarsus I, tibia I, and palpi of male and female of *Angelothrombium pandorae*.[a]

Specimen No.	First leg					Palpi													
	LTaI	HTaI (max)	LTiI	L/H TaI	LTaI LTiI	PALPI: LFe	HFe	LPa	HPa	LTi	HTi (basal)	LTa	HTa (max)	VLPDTi	L/H Fe	L/H Pa	L/H Ti	L/H Ta	VLPDTi LTi
♂ 1365-01	1248	234	1690	5.34	0.74	963	547	442	365	754	260	780	130	468	1.76	1.21	2.90	6.0	0.62
♂ 1365-01	1222	234	1664	5.23	0.73	1014	547	494	365	728	273	780	130	468	1.86	1.36	2.67	6.0	0.64
♂ 1427B	1223	219	1453	5.58	0.84	1014	547	456	324	699	243	710	121	426	1.85	1.41	2.88	5.87	0.61
♂ 1427B	1223	207	1476	5.91	0.83	963	527	486	324	699	263	699	126	405	1.83	1.50	2.66	5.55	0.58
♂ 1427C	1223	230	1615	5.32	0.76	984	552	497	329	791	284	826	152	517	1.78	1.51	2.79	5.43	0.65
♂ 1427C	1223	230	1615	5.32	0.76	989	527	466	324	760	263	831	152	497	1.88	1.44	2.89	5.47	0.65
♂ 1427A	1384	230	1684	6.02	0.82	1044	613	527	355	771	284	811	152	497	1.70	1.44	2.71	5.34	0.64
♂ 1427A	1384	242	1707	5.72	0.81	1044	633	517	370	771	294	796	142	486	1.65	1.40	2.62	5.61	0.63
♂ 1427F1	1223	207	1488	5.92	0.82	1014	552	517	324	710	253	699	106	476	1.84	1.59	2.81	6.59	0.67
♂ 1427F1	1223	207	1476	5.91	0.83	1014	547	497	324	704	263	720	121	446	1.85	1.53	2.68	5.95	0.63
♂ 1427F2	981	173	1142	5.67	0.86	781	446	355	284	578	202	649	101	385	1.75	1.25	2.86	6.43	0.67
♂ 1427F2	969	173	1153	5.60	0.84	801	446	385	273	608	202	649	101	405	1.80	1.41	3.00	6.43	0.67
Means, ♂♂	1210.5	215.5	1513.6	5.63	0.80	968.7	541.0	469.9	330.8	706.1	257.0	745.8	127.8	456.3	1.80	1.42	2.79	5.89	0.64
♀ 1427A	1040	221	1274	4.71	0.82	945	513	405	342	720	261	765	135	477	1.84	1.45	2.76	5.76	0.66
♀ 1427B	936	195	1144	4.80	0.82	909	486	459	306	657	243	693	126	369	1.87	1.50	2.70	5.50	0.56
♀ 1427C	1066	234	1352	4.56	0.79	1071	594	522	374	810	279	837	144	513	1.80	1.40	2.90	5.81	0.63
♀ 1427C	884	221	1170	4.00	0.76	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♀ 1427F	1066	221	1274	4.82	0.84	—	—	—	—	—	—	—	—	—	—	—	—	—	—
♀ 1427F	806	182	1066	4.43	0.76	945	549	504	369	729	261	792	144	459	1.72	1.37	2.79	5.50	0.63
Means, ♀♀	966.3	212.3	1213.3	4.55	0.80	967.5	535.5	495.0	347.8	729.0	261	771.8	137.3	454.5	1.81	1.43	2.79	5.64	0.62

[a]L=length, H=height, Fe=femur, Pa=patella, Ti=tibia, Ta=tarsus, PDTi=pars distalis tibiae, V=ventral, L/H=ratio of length to height. All lengths given in microns. With the exception of ♂ 1365-01 (Holotype), all mites were captured as courting pairs or trios.

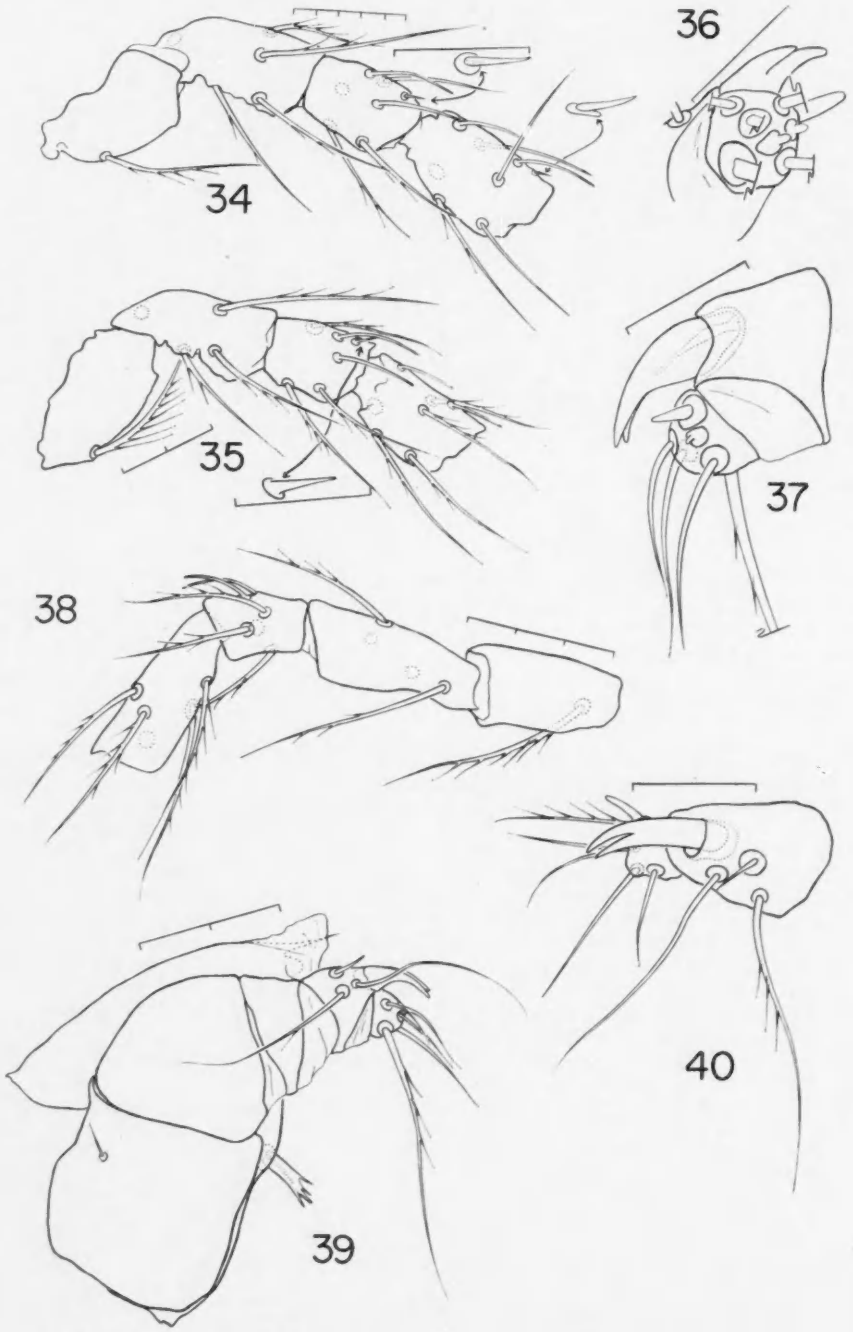
tum with posterolateral setae and sensilla with positions reversed from relationship usually found in the Trombidiidae, the posterolateral setae having become displaced to a position directly between the sensilla. Two flexure lines extending between prosensilla and anterolateral setae, each of these lines forming a large loop at the inner end. Cuticle of scutum with prominent refractile punctae. Ocular plates prominent, bicorneate, the anterior cornea distinctly larger than the posterior. Postscutum with a single pair of long peripectinate setae. At the margins of the body, lateral to the postscutum, a pair of large setigerous sclerites, somewhat like those found in larvae of the genus *Allothrombium*. Other dorsal setae borne on smaller setigerous sclerites; 22 dorsal and marginal postscutal setae, plus 8 ventral postcoxal setae, making a total of 30 postscutal and postcoxal setae (three specimens checked and found to be identical). Punctae on smaller setigerous sclerites fainter than on scutum and postscutum. Membranous cuticle faintly striate and sparsely tuberculate, like the ventral cuticle (fig. 33).

Coxa I with a rather sharp anterior angle, just dorsal to which is the delicate and tapering supracoxal seta. Ventral coxal setae numbering (2–2–1); slender, tapering, elongate, with numerous slender barbs, all of more or less the same form, differing only slightly in length. Cuticle with numerous prominent punctae. Urstigma very small. Intercoxal area marked with very delicate striae, rather widely spaced, and marked at intervals with delicate spherical tubercles (fig. 33). In the region around the anal anlage, the striae are somewhat more closely spaced, and the tubercles are smaller and less refractile. Anal anlage very small, slightly more than halfway between the medial angles of coxae III and the posterior margin of the body. Intercoxal area with a single pair of setae between coxae III, unusual in that they are significantly longer than the neighboring setae on III. No trace of a

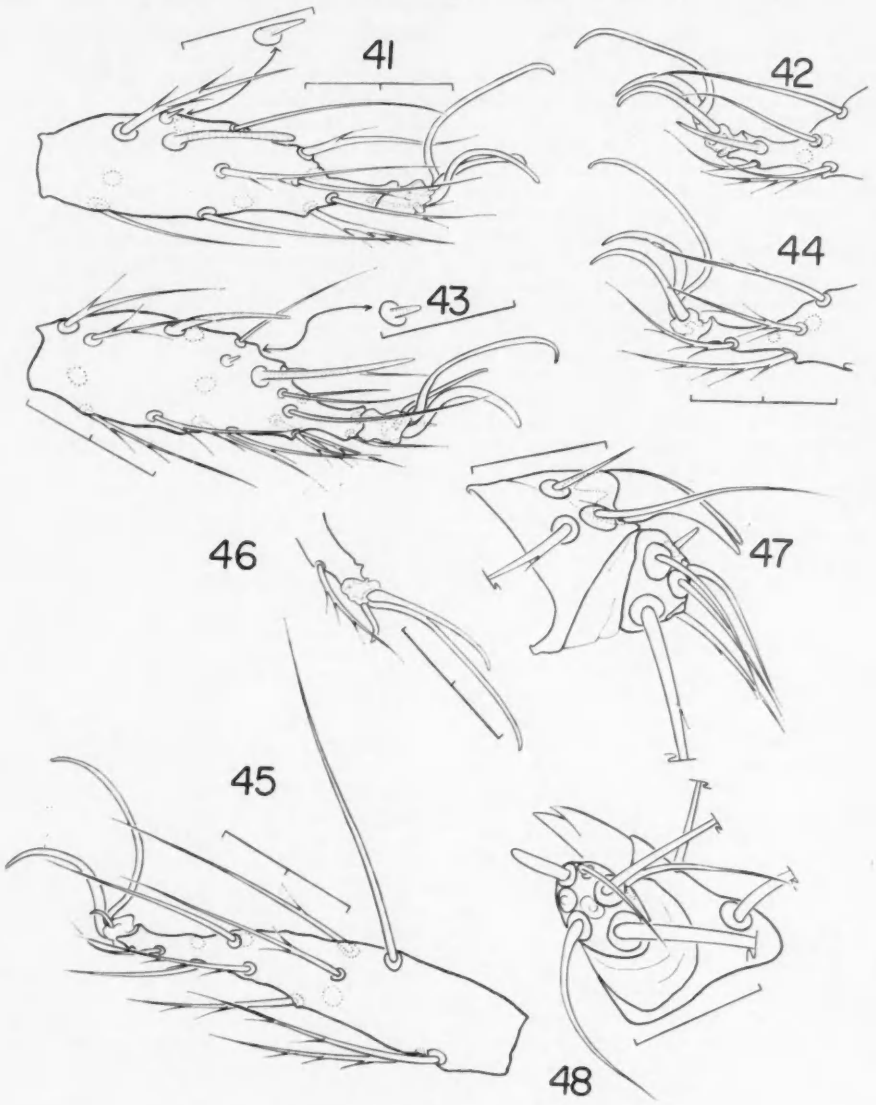
Table 2.—Chaetotaxy of legs of *Angelothrombium pandorae*[a]

Leg	tr	fe	pa			ti			ta			
	n	n	s	v	n	s	v	n	s	e	f	n
I	1	5	2	1	4	2	1	5	1	2	1	17
II	1	4	2	1	3	2	0	5	1	0	1	14
III	1	4	2	0	3	0	0	5	0	0	0	13

[a]e=eupathidia, f=famulus, fe=femur, n=normal setae, pa=patella, s=solenidia, ta=tarsus, ti=tibia, tr=trochanter, v=vestigial setae.



FIGS. 34–40.—*Angelothrombium pandorae*, new species, larva. FIG. 34.—Trochanter-tibia I, anterior. FIG. 35.—Trochanter-tibia II, anterior. FIG. 36.—Tibia and tarsus of palp, terminal view. FIG. 37.—Tibia and tarsus of palp, anterior. FIG. 38.—Trochanter-tibia III. FIG. 39.—Detail of gnathosoma, lateral view. FIG. 40.—Tibia and tarsus of palp, dorsal.



EXPLANATION OF PLATE VI

FIGS. 41–48.—*Angelothrombium pandorae*, new species, larva. FIG. 41.—Tarsus II, left, anterodorsal. FIG. 42.—Tip of tarsus I, posterior. FIG. 43.—Tarsus I, left, anterodorsal. FIG. 44.—Tip of tarsus II, posterior. FIG. 45.—Tarsus III, posterior. FIG. 46.—Tip of tarsus III, anteroventral. FIG. 47.—Tibia and tarsus of palp, posterior. FIG. 48. Tibia and tarsus of palp, distiventral.

Lassenia-organ was found between coxae II and III.

Base of gnathosoma (fig. 39) with very delicate supracoxal setae tapering abruptly at the middle. No trace of trochanter present, palpi four-segmented. Femur and patella lacking setae. Tibia with a slender seta posteriorly bearing four delicate barbs; also a short, smooth seta dorsally, and a longer smooth seta distally. In addition to these three setae, the tibia bears the very heavy bifurcate odontus.

The tarsus is reduced to a small hemispherical knob. From the posterior aspect (fig. 47) can be seen a long ventral seta bearing four or five slender barbs, and dorsal to this the insertions of two smooth setae, the dorsalmost of which is

shorter than the other. On the anterior aspect of the tarsus there is a stout, usually digitiform seta dorsally (fig. 37). One very slender, smooth distal seta and a slender ventral seta bearing two or three very delicate barbs make up the total complement of six longer setae on the palp. In addition to these six setae, there are two alveoli which are best seen in direct end-on view (figs. 36, 48). In some cases it appears questionable whether or not any trace of a shaft is present, but in other cases there is no doubt that at least a short shaft approximately 0.7μ–1.0μ long is present (fig. 37). However, these are usually visible only in the most favorably oriented material and are especially difficult to see in side view without careful search. No typical eupathidia and no solenidia have been found on the palpal tarsus of the larvae of this species. Chelicerae short, compact, with a pair of gently curved apodemes attached posteroventrally. Tarsus of chelicera smooth along dorsal margin.

Velum very simple. Protorostral setae curving sharply inward toward midline, then with distal half strongly curved in an anterolateral direction. No indication of deutorostral setae, but tritorostral setae well developed, heavy, spikelike, with six to eight irregular teeth in distal one-third. Podocephalic canals extending to level of middle of coxa I; with a delicate posterior branch about one-third of the way between the cheliceral apodemes and the end of the canal.

Femora I–III undivided, all legs with only five free segments beyond the coxa. Patella I with two solenidia (s_3 and s_4) at 0.50–0.52, and at 0.52–0.61. Vestigial seta at 0.74–0.80. Patella II with solenidia$_3$ at 0.49–0.59 and 0.62–0.69; vestigial seta at 0.73–0.80. Tibia I with s_3 at 0.31–0.33 and s_4 at 0.78–0.80; vestigial seta at 0.83–0.87. S_4 is only slightly larger than s_3. The vestigial setae are moderately long and taper to a rather sharp point. Tibia II with s_3 at 0.35–0.36 and 0.75–0.79. Although s_4 of tibia II is characteristically longer than s_3, there are no other differences apparent in the structure of these two setae. Patella III with two solenidia at 0.58–0.60, the two usually lying at the same level. Tarsus I with s_1 at 0.35–0.40 (av. 0.375), f_1 at 0.43–0.51 (av. 0.470), e_d at 0.58–0.62 (av. 0.596), e_p at 0.85–;.88 (av. 0.868), and a smooth normal seta at 0.51–0.58 (av. 0.536). The latter is characteristically more erect than the other normal setae and only rarely bears a single barb. E_d lacks a companion seta. S_1 shows prominent internal bands, but e_d and e_p are structureless. Normal setae of tarsus I rarely with more than six very long, slender barbs, and frequently with none, one, or two in the case of the smaller and more distal normal setae. Tarsus II with s_2 at 0.33–0.40 (av. 0.357), f_2 at 0.25–0.44 (av. 0.335), and a smooth erect normal seta at 0.38–0.52 (av. 0.478). The foregoing ranges and averages for the positions of the tarsal setae were based on 10 tarsi in each case, while the ranges for the setae on the more proximal segments of the legs were based on only two segments in each case. S_2 is characteristically different from s_1 in that instead of tapering uniformly, it reaches its narrowest point some distance back from the tip and is slightly clavate beyond that point. Also, it is more strongly flared at the base. The position of f_2 is quite variable. In most cases it is somewhat proximal to s_2, but in two of the ten cases observed it was inserted distally to the alveolus of s_2. The three claws on each tarsus are unequal. The anterior claw on all tarsi is rather uniformly curved and the shaft is moderately thick; the median claw is relatively more slender than the anterior claw, more erect, and the middle portion of the shaft is relatively straight rather than uniformly curved. The posterior claw on tarsi I and II is quite straight in the basal half and uniformly curved in the distal half; on III it is very short and only slightly curved, but not otherwise modified except that it is oriented away from the median axis of the tarsus (fig. 46). Other details of chaetotaxy of legs approximately as shown in table 2.

TYPE LOCALITY.—2.0 miles northwest of Rancho Mirage, Riverside County, California. The larvae were taken in fine sand at a depth of about 9 inches, June 2, 1958, collected by the writers. The adults described above were taken on the surface of fine sand, or at a depth of 3 to 4 inches.

The correlation of the larva of this species with the adult was established by rearing. The adults were placed in buckets buried in the sand in February, and the eggs hatched in late May and early June. In host attachment tests, the larvae of this species were found to attach to Diptera, Hemiptera and Orthoptera. In the field, however, larvae have been found only on grasshoppers. Apparently a number of species of Locustidae are satisfactory as hosts. The habits of the adults are not adequately known, but they are predators on termites. Studies on the biology of this species are still in progress and will be presented in a subsequent paper by the writers.

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A NEW CLASSIFICATION OF THE PAEDOGENIC GALL MIDGES FORMERLY ASSIGNED TO THE SUBFAMILY HETEROPEZINAE (DIPTERA: CECIDOMYIIDAE)[1]

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ABSTRACT

Recognition of the subfamily Heteropezinae is not justifiable, as the genera that have been included may be reassigned to tribes in both the Lestremiinae and the Cecidomyiinae. In the proposed new classification nine tribes are recognized in the Lestremiinae and all are characterized, as is the tribe Leptosynini of the Cecidomyiinae. The following tribes either are new or represent a new status: MOEHNIINI, for **MOEHNIA** (type *M.* **erema,** California); HETEROPEZINI (=Heteropezinae Schiner, =Heteropezidae Enderlein, =Oligarcinae Enderlein), for *Heteropeza* Winnertz and **HETEROPEZINA** (type *H.* **cathistes,** Florida); ACOENONIINI, for *Acoenonia* Pritchard; MIASTORINI (=Miastorinae Enderlein), for *Miastor* Meinert (=*Peromiastor* Kieffer, n. syn.); and LEPTOSYNINI (=Leptosyninae Enderlein), for *Leptosyna* Winnertz, *Frirenia* Kieffer, *Brittenia* Edwards, and **BARNESINA** (type *B.* **hylecoites,** California; also included, *B.* **quercivora** (Felt) (*Leptosyna q.* Felt, =*Leptosyna americana* Felt, n. syn.)). Other new synonymy: *Heteropeza pygmaea* Winnertz (=*Oligarces noveboracensis* Felt) and *Miastor metraloas* Meinert (=*M. hospes* Winnertz, =*M. subterraneus* Karsch, =*M. americana* Felt, =*M. hastatus* Kieffer, =*M. similis* Kieffer, =*Peromiastor dryobius* Kieffer).

Paedogenesis, the reproduction of larvae by a mother larva, is an entomological phenomenon well known to students of biology. Ovoviviparous gall midge larvae have been found living gregariously under the bark of logs and stumps showing incipient decay, in rotting and damp wood, in mushrooms, mushroom spawn, or mushroom compost, in decaying leaves, manure, and on the surface of moist paper flower pots. When conditions are not favorable for this type of reproduction, adult midges are formed for dissemination of the species.

Miastor metraloas Meinert (=*M. americana* Felt) has been studied in particular with regard to this unusual type of reproduction. But other gall midges exhibit paedogensis. The genus *Mycophila* Felt in the lestremiine tribe Micromyini is biologically characterized by paedogenesis; the remaining genera known to have this reproductive ability have been assigned to the subfamily Heteropezinae. It is thus established that paedogenesis is not a monophyletic character within the family Cecidomyiidae, and the present study indicates that it has arisen independently in several different evolutionary lines.

Schiner (1868) proposed the subfamily Heteropezinae[2] on a basis of the genus *Heteropeza* Winnertz. Kieffer (1894, 1898) recognized the subfamily for *Heteropeza* and several other paedogenic genera as well as cecidomyiine genera, and later (1913) he included several micromyine genera. Felt (1911, 1913, 1925, 1931, 1958) based his conception of the subfamily Heteropezinae mainly on the absence of circumfila, and he included the paedogenic genera and several cecidomyiinae genera. Brues and Melander (1932), Mani (1946), and Rao (1955) essentially followed Felt.

Kertész (1902) restricted the group to genera now known to be paedogenic, and Enderlein (1936) did likewise but elevated it to family rank. Edwards (1941) also restricted the subfamily to those forms capable of paedogenesis, except for the genus *Mycophila*.

The discovery of a new genus, *Moehnia*, closely allied to *Heteropeza* but with more primitive wing venation and tarsal segmentation, shows that *Heteropeza* is actually a member of the subfamily Lestremiinae. Moreover, the nonpaedogenic larva of *Heteropeza* has a sclerotized, circular, and terminal anal opening as in the Lestremiinae. The genus *Miastor* also agrees essentially with lestremiine characteristics.

The other paedogenic genera, *Leptosyna* Kieffer, *Frirenia* Kieffer, and *Brittenia* Edwards, that have been placed in the Heteropezinae were excluded from the Cecidomyiinae by Edwards (1941) because of the noncircumfilar flagellar sensoria of the females known to him and the presence of pigmented spermathecae. These characters, however, are actually known to occur in the Cecidomyiinae (in *Winnertzia* Rondani and *Parwinnertzia* Felt) and present no reasons for exclusion of these genera from that subfamily, particularly, as noted by Edwards, with the close agreement of other characters such as the tarsal segmentation, the eyes, and the wing vestiture. Moreover, the female of *Barnesina*, a new genus closely related to *Leptosyna* Kieffer, has a circumfilum on each flagellar segment as in the Cecidomyiinae. These genera are here considered as constituting a tribe of the Cecidomyiinae.

Thus there is no justification for recognizing a third subfamily, the Heteropezinae, in the family Cecidomyiidae. There are two ancient lines of

[1]Accepted for publication July 7, 1959.

[2]It is interesting to note that Schiner based this concept on a gall-making, nonpaedogenic species that was erroneously referred to the genus *Heteropeza*.

development, the Lestremiinae and the Cecidomyiinae, and each of these groups is divisible into well defined tribes.

No consideration is here given to the five genera described from specimens in amber and copal and assigned to the Heteropezinae. Their characterizations are inadequate for critical evaluation.

Of the recent genera that have been assigned to the Heteropezinae by various workers, *Trichopteromyia* Williston and *Ceratomyia* Felt belong in the lestremiine tribe Micromyini. *Epimyia* Felt and *Brachyneura* Rondani belong in the cecidomyiine tribe Brachyneurini. *Gioliella* Del Guercio was originally assigned to the Oligotrophini and should be considered in connection with that tribe. *Tetradiplosis* Kieffer and Jörgensen was assigned by Kieffer (1913) to the Cecidomyiini. *Brephometra* Strand (= *Pero* Meinert, = *Meinertomyia* Felt) is a *nomen dubium*.

The genera *Necrophlebia* Skuse, *Chastomera* Skuse, *Johnsonomyia* Felt, and *Kronomyia* Felt all should be relegated to the Porricondylini (Epidoseini), at least until there is a modern revision of that tribe.

Haplusia Karsch, *Neohaplusia* Rao, and *Haplusiella* Rao represent higher forms of the Cecidomyiinae, and should be considered in connection with the Oligotrophini.

Klyver (1931) reported larval paedogenesis and oviparous pupae of a gall-making midge on leaves of lupine in California. My study of these midges, also from South San Francisco on *Lupinus nana*, shows them to be *Dasineura* near *trifolii* Loew, and they have reproduction only by adult females.

Epourenia Rapp (1946) was based on a single species, *E. viva* Rapp, and the genus was referred to the Heteropezinae. The drawing of the single female on which the species name was based indicates that *Epourenia* is a synonym of the oligotrophine genus *Rhabdophaga* Westwood.

The remainder of the genera assigned to the Heteropezinae, those in which paedogenesis occurs, are treated in detail in this article, and the North American species belonging to these genera are also discussed in detail. In order to clarify the disposition of these genera, all of the tribes of the Lestremiinae are characterized and keys are presented for their recognition.

ACKNOWLEDGMENTS

I am indebted to Dr. Richard Foote for permission to re-examine certain of Felt's types, and to Dr. H. F. Barnes, Dr. M. J. D. White, Dr. J. W. MacSwain, Dr. Bruce Nicklas, Dr. D. Elmo Hardy, Mr. W. C. Bentinck, and the late Dr. F. W. Edwards for other specimens of paedogenic midges that were used in this study. Mrs. Celeste Green kindly delineated the illustrations.

Family **Cecidomyiidae** Macquart 1838

KEY TO SUBFAMILIES

1. Tarsus with first segment longer than second segment or with less than five segments ..... **Lestremiinae**
   Tarsus with five segments, the first shorter than the second ..... **Cecidomyiinae**

Subfamily **Lestremiinae** Rondani 1840

KEY TO TRIBES

1. Tarsus with five segments 2
   Tarsus with less than five segments 10
2. Apterous or brachypterous 3
   Alate 4
3. Ocelli two; legs without scales ..... (3) **Lestremiini**
   Ocelli three; legs with scales ..... (9) **Micromyini**
4. Cu forked, with Cu_1 arising near middle of Cu; M_{3+4} absent or nearly so 5
   Cu simple; M_{3+4} distinct 7
5. Tibiae with distoventral spines; R_5 abbreviated, reaching costa well before end of wing 6
   Tibiae without distoventral spines; R_5 reaching apex of wing ..... (9) **Micromyini**
6. Tibia with two ventrodistal spines; M_1 and M_2 present; eyes with dorsomedian bridge devoid of facets ..... (5) **Moehniini**
   Tibia with a row of ventrodistal spines; M_{1+2} present; eyes without lateral bridges, leaving a large dorsal eye ..... (8) **Acoenoniini**
7. M_{3+4} arising from M; flagellum with scattered bristles and setae ..... (1) **Catotrichini**
   M_{3+4} free; flagellar segments each with a whorl of bristles 8
8. Ocelli three; humeral cross-vein absent; medial fork shorter than stem or absent 9
   Ocelli two or none; humeral cross-vein present; medial fork longer than stem ..... (3) **Lestremiini**
9. M_{1+2} forked; PCu free ..... (2) **Catochini**
   M_{1+2} simple, evanescent distally; PCu united with Cu ..... (4) **Strobliellini**
10. Tarsus with four segments; R_5 present ..... (7) **Miastorini**
    Tarsus with two or three segments; R_5 absent ..... (6) **Heteropezini**

1. Tribe **Catotrichini** Edwards

CATOTRICHINI Edwards 1938: 102; Pritchard 1948: 662; Pritchard 1953: 126.
CATOTRICHIARIAE Mani 1946: 191.

The generalized wing venation is characteristic of the tribe Catotrichini. It may readily be recognized by the distinct subcosta and humeral cross-vein.

Head orbicular. Eyes separated by ocellar tubercle. Ocelli three. Palpus with four segments, all bearing sensory setae. Antenna with 2+14 segments; male flagellar segments subbinodose, the distal swelling on the long neck of each segment and the proximal enlargement bearing scattered sensory setae; female flagellar segments each with a slight neck and with scattered sensory setae. Legs with microchaetae and numerous tactile setae; tibia without ventrodistal spines; tarsus with five segments; claws nearly straight, with proximoventral teeth; empodium short. Wing membrane with microtrichia and macrotrichia; C extending around wing, the margin without a break; h present; Sc present, including Sc_2; R_1 and R_s present; R_5 reaching

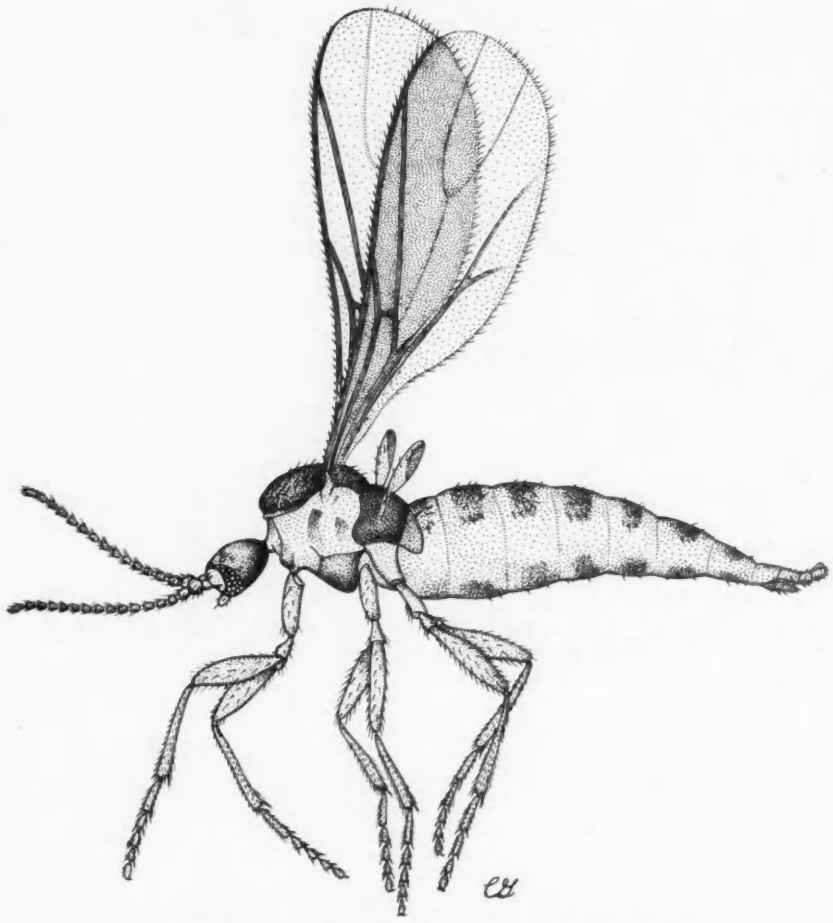

FIG. 1.—*Moehnia erema:* lateral aspect of female (paratype).

beyond tip of wing; r-m forming a strong angle with R_5; M_{1+2} branched; M_{3+4} distinct, arising from M; cu simple; PCu free; Pl present. Hypopygium with ninth tergum large and bilobed; tenth tergites very small and hidden; genital rod present. Female with two sclerotized spermathecae.

The tribe Catotrichini contains a single genus, *Catotricha* Edwards (1938), and three species of which two are North American and one Japanese. Edwards (1938) and Pritchard (1948, 1953) discussed these species.

2. Tribe **Catochini** Edwards

CATOCHINI Edwards 1938: 104; Pritchard 1948: 663.
CATOCHARIAE Mani 1946: 191.

Members of the tribe Catochini may be recognized by the short medial fork.

Head orbicular. Eyes confluent dorsally, the lateral portion sometimes devoid of facets. Ocelli three. Palpus with four segments, the first with sensory rods. Antenna with 2+6 to 14 segments; flagellar segments of male usually with necks, the enlargements each with a proximal whorl of tactile setae and distal sensory setae or processes; flagellar segments of female with short necks or none, each with a whorl of short setae proximally, a whirl of long sensory setae, and sensory rods or processes distally. Legs with microchaetae and numerous tactile setae; tibia without ventrodistal spines; tarsus with five segments; claw slightly curved; empodium short. Wing with microtrichia and with macrotrichia at least on some veins; costa ending just beyond R_1 or just before M_1 with a break in the margin at its end; h absent; Sc absent; R_1 long; R_s very short; r-m forming an angle with R_s; R_5 reaching C before or at end of wing; M_{1+2} branched, the fork shorter than the stem; M_{3+4} present except at base or arising from base of M; Cu simple; PCu present; P1 absent.

Hypopygium with ninth tergum large; anal lobes small and hidden; genital rod present. Female with two sclerotized spermathecae.

The tribe Catochini contains six genera. The European and North American species were considered in the tribal revisions by Edwards (1938) and by Pritchard (1948). A single species is known from India.

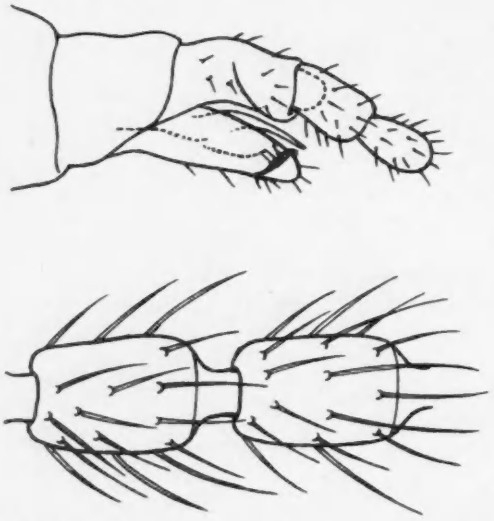

FIG. 2.—*Moehnia erema:* lateral aspect of ovipositor and sixth and seventh flagellar segments of female (paratype).

3. Tribe **Lestremiini** Kieffer

LESTREMIDES Kieffer 1898: 52.
LESTREMIARIAE Kieffer 1901: 451; Kieffer 1913b: 305.
LESTREMIINARIAE Kertész 1902: 11; Felt 1908b: 309; Felt 1913: 129; Felt 1918: 296; Felt 1925: 136; Felt 1931: 425; Mani 1935: 378; Mani 1946: 191.
LESTREMINARIAE Felt 1911a: 31.
LESTREMIINI Enderlein 1911: 189; Enderlein 1912: 263; Edwards 1938: 24; Pritchard 1951: 241; Pritchard 1953: 126.
LESTREMIINAE Enderlein 1936: 59.

The tribe Lestremiini may be recognized by a long medial fork and a simple cubitus.

Head oribuclar. Eyes confluent dorsally. Ocelli two or none. Palpus with three or four segments, the first with sensory rods. Antenna with 2+6 to 12 segments; male flagellar segments usually with distal necks, each enlargement with a proximal row of tactile setae, usually a crenulate whorl of long sensory setae, and sensory setae or processes distally; female with flagellar segments ovate or with short necks, each with a proximal whorl of tactile setae and with distal sensory setae or processes. Legs with microchaetae and numerous tactile setae or narrow scales; tibia without ventrodistal spines; tarsus with five segments; claws variously modified; empodium usually well developed. Wing with membrane covered with microtrichia and with macrotrichia at least at tip; C ending abruptly at or just beyond end of R_5 and the margin there broken; h present; Sc free; R_1 distinct; R_s short or obliterated; R_5 not reaching end of wing; M_{1+2} forked, the fork longer than the stem; M_{3+4} present except at base; Cu simple; PCu free; Pl present. Hypopygium with ninth tergum membranous; tenth tergal lobes well developed; genital rod present. Pigmented spermathecae absent or a single pale spermatheca present.

Edwards (1938) redescribed the European species of the tribe Lestremiini, and Pritchard (1951) revised the classification of the species known from North America. Eight genera are recognized, and there are a number of species. Known distribution includes Europe, North Africa, North America, the West Indies, New Zealand, Samoa, and India.

4. Tribe **Strobliellini** Kieffer

STROBLIELLINAE Kieffer 1898: 51; Enderlein 1912: 263; Enderlein 1936: 61.
STROBLIARIAE Kieffer 1901: 451.
STROBLIELLINARIAE Kertész 1902: 11.
STROBLIELLARIAE Kieffer 1913b: 304.
STROBLIELLINI Edwards 1938: 107.

In the tribe Strobliellini R_5 is simple, evanescent distally, and Cu is simple.

Eyes confluent dorsally. Ocelli three. Palpus with four segments. Antenna with 2+more than 20 segments (male) and 2+23 segments (female); flagellar segments with distal stems, each enlargement with a whorl of short setae proximally, a whorl of long setae, and with distal sensory setae. Legs with tactile hairs; tibia without distal spines; tarsus with five segments; claws simple; empodium very short. Wings with dense macrotrichia; C continuing well beyond R_5 but without a break in the margin; h absent; Sc free; R_1 long; R_s forming a right angle with R; R_5 reaching end of wing; M_{1+2} simple, evanescent distally; M_{3+4} present, free; Cu simple; PCu fused with Cu; P1 short. Hypopygium with ninth tergum large; anal tergites small and hidden; genital rod present. Sclerotized spermathecae two.

The tribe Stroliellini is based on the genus *Strobliella* Kieffer and a single species, *S. intermedia* Kieffer (1898), occurring in Europe. Edwards (1938) redescribed this species.

5. **Moehniini,** new tribe

The tribe Moehniini is characterized by the abbreviated R_5; the presence of a medial fork although faint; the absence of M_{3+4} except at its very base; the presence of Cu_1, arising near the middle of Cu; and the presence of a pair of distoventral spines on the tibia. There are five tarsal segments.

Moehnia, new genus

Type of genus: *Moehnia erema*, new species.

Head elongate. Ocelli three, of equal size.

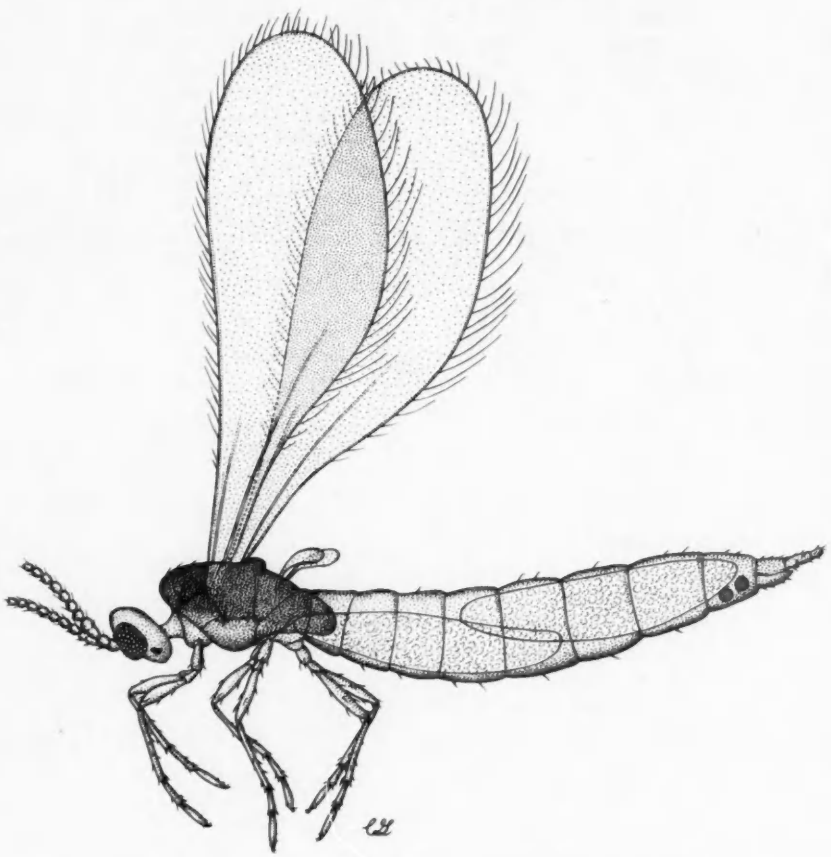

FIG. 3.—*Heteropeza pygmaea:* lateral aspect of female (Berkeley, California).

Eyes with a narrow dorsal bridge. Palpus a single segment bearing sensory setae. Antenna of female with 2+12 segments; flagellum with only irregularly scattered, acute setae. Femora with microchaetae and tactile setae and each of similar lengths; tibiae with short tactile setae, and each with a pair of sparsely rayed distoventral spines; tarsus with five segments, the first twice as long as the second; claws strongly bent; empodium rudimentary. Wing membrane without macrotrichia; costa extending nearly to M_1 and without a definite break in the wing at its termination; humeral cross-vein and Sc absent; R_1 not extending to middle of wing; R_s forming an angle with R; R_5 reaching C well before end of wing; M_1 and M_2 separate but very faint like M_{1+2} the fork about as long as the stem; M_{3+4} present only at extreme base; Cu_1 a branch of Cu_2 beyond middle of Cu; PCu fused with Cu; P1 indistinct; anal angle not developed. Sclerotized spermathecae absent.

The male is unknown.

This genus is named in honor of Dr. Edwin Möhn, Staatl. Museum für Naturkunde, Stuttgart, Germany.

Moehnia erema, new species

(Figs. 1, 2)

FEMALE.—Eye bridge one facet wide at junction. Antenna with pedicel enlarged, rounded; flagellar segments each about twice as long as broad and with a short but distinct distal stem. Tarsal claw with a slight tooth on inside just beyond bend. Length of wing 0.6 mm.

HOLOTYPE.—Female, Berkeley, California, August 1958 (A. E. Pritchard and J. W. MacSwain); in the Pritchard collection.

PARATYPES.—Thirty-four females on slides (and several hundred females in alcohol), Berkeley, California, August 1958 (A. E. Pritchard and J. W. MacSwain).

Thousands of adults of this midge appeared in

an entomology office-laboratory over a period of a few days, apparently emerging from a steam-pipe tunnel. The presence of no more than several very large eggs in each female indicates that this species is paedogenic.

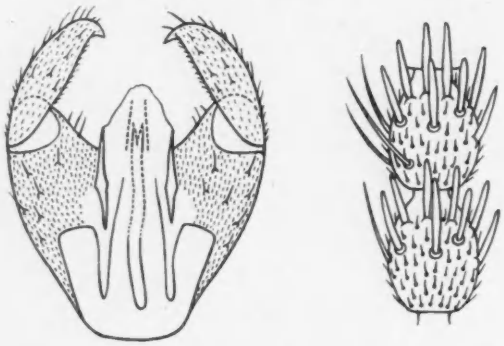

FIG. 4.—*Heteropeza pygmaea:* dorsal aspect of hypopygium, with 9th and 10th tergites removed, and fourth and fifth flagellar segments of female (Wye, England).

6. Tribe **Heteropezini** Schiner

HETEROPEZINAE Schiner 1868: 5; Kieffer 1898: 53; Kieffer 1901: 449; Kertész 1902: 1; Felt 1911c: 84; Felt 1913: 202; Kieffer 1913b: 310; Felt 1925: 138; Felt 1931: 299; Brues and Melander 1932: 275; Enderlein 1936: 64: Edwards 1941: 1; Mani 1946: 194; Rao 1955: 221; Felt 1958: 89.
HETEROPEZIDAE Enderlein 1936: 63.
OLIGARCINAE Enderlein 1936: 64.

The tribe Heteropezini is unique in that the wing bears no distinct veins, and the tarsus consists of only two or three segments. The presence of a pair of distoventral spines on the tibia, the elongate head, and only irregularly placed sensory spines on the female flagellum indicates a close relationship with the Moehniini.

Head elongate, the lateroventral angles with internal pigment spots (lost in KOH treatment). Eyes rounded, lateral, with large facets, and without a dorsal bridge. Ocelli absent. Palpi absent. Antenna of male with 2+9 segments, the flagellum with one or two tactile setae and irregularly scattered sensory spines; female antenna with 2+7 to 9 segments, the flagellar sensoria awl-like or blade-like. Legs with microchaetae and a few tactile setae; tibia with two ventrodistal spines; tarsi with two or three segments the proximal of which bear ventrodistal spines; claws simple, scarcely curved; empodium absent. Wings with only microtrichia on membrane; costa continuous around wing and margin without a break; base of R_1 and Cu faint, the other veins absent. Genital rod present. Spermathecae two, sclerotized.

KEY TO GENERA

1. Tarsus with two segments ..... **Heteropeza**
   Tarsus with three segments ..... **Heteropezina**

Genus **Heteropeza** Winnertz

Heteropeza Winnertz 1846: 13; Winnertz 1870: 4; Karsch 1877: 16; Skuse 1888: 57; Rübsaamen 1892: 401; Felt 1911a: 36; Felt 1913: 209; Kieffer 1913b: 312; Edwards 1937: 145; Edwards 1941: 2. Type of genus: *Heteropeza pygmaea* Winnertz; monobasic.
Oligarces Meinert 1865c: 237; Rübsaamen 1892: 403; Felt 1911a: 38; Felt 1913: 223; Kieffer 1913b: 311. Type of genus: *Oligarces paradoxus* Meinert; monobasic.

The genus *Heteropeza* may be recognized by the biarticulate tarsi. Edwards (1937) pointed out that *Oligarces paradoxus* Meinert is a synonym of *Heteropeza pygmaea* Winnertz, the only species known in Europe. Two species are known in North America. *Heteropeza transmarina* Schiner, based on a female from Australia, was incorrectly assigned to this genus.

KEY TO SPECIES

Males

1. Distiforceps with a terminal cusp ..... **pygmaea**
   Distiforceps without a terminal cusp ..... **ulmi**

Females

1. Flagellum with nine segments ..... **pygmaea**
   Flagellum with eight segments of which the first two may be united ..... **ulmi**

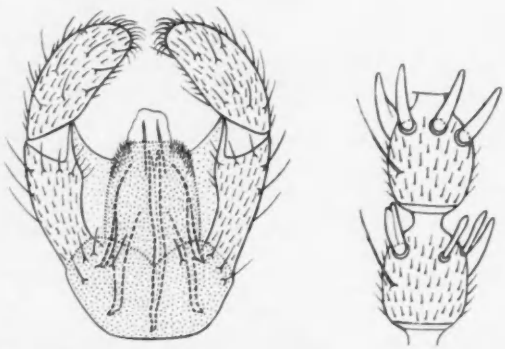

FIG. 5.—*Heteropeza ulmi:* dorsal aspect of hypopygium (lectotype) and fourth and fifth flagellar segments of female (Honolulu, Hawaii).

Heteropeza pygmaea Winnertz

(FIGS. 3, 4)

Heteropeza pygmaea Winnertz 1846: 13; Winnertz 1870: 4; Edwards 1937: 145; Edwards 1941: 2.
Oligarces paradoxus Meinert 1865c: 238; Rübsaamen 1892: 404.
Oligarces noveboracensis Felt 1907: 5; Felt 1908a: 286; Felt 1913: 223. Monotype, female, Albany, New York, July 15, 1907; in the Felt collection. NEW SYNONYMY.
Heteropeza noveboracensis, Felt 1958: 92.

The monotype female of *noveboracensis* has 11 antennal segments, not 13 as described by Felt. This female and others from the United States are indistinguishable from European specimens representing *Heteropeza pygmaea*.

Specimens studied are from Birmingham, Engr land, reared from woodwork of a Wolseley motocar by D. L. Gunn (recorded by Edwards 1937); Wye, Kent, England, reared from mushroom by B. D. Moreton; Brayton, Selby, Yorks, England,

March 2, 1956, reared from mushroom by Stanley Middlebrook; Yaxley Sidings, Peterborough, Northants, England, May 17, 1956, reared from mushroom by F. C. Atkins; Albany, New York, July 15, 1907 (monotype of *noveboracensis*); Missouri, reared from mushroom compost by Leonard Haseman; Kennett Square, Pennsylvania, August 5, 1947, reared from mushroom spawn by M. J. D. White; Berkeley, California, January 14, 1952, reared from rotten log by J. W. MacSwain; Oakland, California, January 25, 1952, reared by W. C. Bentinck; and Alpine, New Jersey, fall 1958, reared from decaying white oak and white birch logs by R. Bruce Nicklas.

Heteropeza ulmi (Felt)

(Fig. 5)

Oligarces ulmi Felt, 1911b: 477; Felt 1913: 224. Lectotype: male, Nassau, New York, April 27, 1911, by present designation; in the Felt collection.
Heteropeza ulmi Felt 1958: 92.

The male of *Heteropeza ulmi* differs from that of *pygmaea* in that the distiforceps are plump, without a terminal cusp, and the sides of the tegmen curve inward rather than being parallel-sided. The female has only eight flagellar segments, on each of which, except the last, the sensoria are comparatively few in number and broadly blade-like. The first two flagellar segments of the female are closely associated, and they may be partially or completely fused. Both sexes are considerably larger than *H. noveboracensis*.

This species has previously been known only from specimens reared from partly decaying elm bark, Nassau, New York. An additional female studied is from Honolulu, Hawaii, September 26, 1957 (M. S. Adachi).

Heteropezina, new genus

Type of genus: *Heteropezina cathistes*, new species.

The genus *Heteropezina* closely resembles *Heteropeza*, but there are three tarsal segments. The male is unknown.

Eyes rounded, widely separated dorsally. Ocelli absent. Palpi absent. Antenna of female with 2+9 segments, the flagellar segments each with one or two tactile setae and many sensory setae. Wings with costa continuous around margin, with long marginal cilia, and with only microtrichia on membrane; R and Cu present proximally. Legs with microchaetae, the femora and tibia with a few tactile setae and each tibia with a pair of ventrodistal spines; tarsus with three segments, the first longer than the second and the first two together about as long as the third and each with a pair of ventrodistal spines; claws simple, slightly curved; empodium absent. Spermathecae two, pigmented. Ovipositor with proximal segment of each lamella fused with tenth tergites.

Heteropezina cathistes, new species

Heteropezina cathistes agrees closely with the description of *Heteropeza pulchella* Meunier (1904) from Baltic amber. However the flagellum of the female has nine rather than eight segments.

FEMALE.—Flagellum with nine segments, the first two segments associated; flagellar sensoria narrowly awl-like and numerous; the third through eighth segments broader than long and each with a slight distal neck, the ninth segment ovate and longer than broad. Spermathecae round and each with short pigmented neck of the sperm duct. Length of wing 0.8 mm.

HOLOTYPE.—Female, Tampa, Florida, September 18, 1945 (Baker); in the Pritchard collection.

PARATYPE.—Female, Tampa, Florida, September 18, 1945 (Baker).

Both of the specimens were combed from the fur of a Norway rat in an old frame barbershop. The holotype contains two eggs that fill the abdominal region, indicating paedogenesis.

7. Tribe **Miastorini** Enderlein

MIASTORINAE Enderlein 1936: 64.

The tribe Miastorini is unique in possessing four tarsal segments. The rounded lateral eyes, the absence of ocelli, the reduction in wing venation, the reduction in the number of tarsal segments, and the similarity of the male hypopygium all indicate a relationship with the Heteropezini. However, R_5 is present, and the distoventral spines on the tibia and proximal tarsal segments are not differentiated.

Head globular, with an internal pigment spot behind each eye. Eyes rounded, lateral, without a dorsal bridge. Ocelli absent. Palpus with one or two segments, with terminal sensory spines. Antenna with 2+9 segments; flagellar segments elliptical, each bearing a sparse whorl of long tactile setae; male with proximal flagellar segments each bearing distally an elongate sensory blade and several sensory rods, the penultimate two segments each with a long sensory seta and several sensory rods, the terminal segment with terminal sensory setae; female with flagellum similar to male except each with a pair of irregularly hastate sensory blades distally. Wing membrane with microtrichia only; C narrowing beyond R_5 and without a break in the margin; h absent; Sc very faint; R_1 present, short; R_s absent; R_5 reaching end of wing; M absent except as base of R; Cu simple, evanescent distally; PCu absent (or fused with Cu); P1 absent. Legs with microchaetae and tactile setae; tibia with weak ventrodistal spines; tarsus with four segments; claws gently curved; empodium broad. Hypopygium with ninth tergite membranous; tenth tergites well developed; genital rod long. Two sclerotized spermathecae.

The tribe Miastorini is based on a single genus.

Genus **Miastor** Meinert

Miastor Meinert 1865a: 42; Winnertz 1870: 5; Karsch 1877: 14; Skuse 1888: 58; Rübsaamen 1892: 403; Felt 1911a: 36; Felt 1913: 205; Kieffer 1913b: 313; Edwards 1941: 2. Type of genus: *M. metraloas* Meinert; monobasic.

Peromiastor Kieffer 1913a: 54; Kieffer 1913b: 312. Type of genus: *P. dryobius* Kieffer; monobasic.

Peromiastor was differentiated from *Miastor* solely on a basis of having a single palpal segment rather than two. In two males of *Miastor metraloas* from Minnesota, each has the palpus with a single segment on one side and with two segments on the other side. This character has therefore neither generic nor specific value.

A single species of *Miastor* is common in western Europe and the eastern United States. *Miastor procax* Skuse (1888) and *M. mastersi* Skuse (1888), from near Sidney, Australia, are not correctly assigned generically inasmuch as both species are described as having five tarsal segments. *Miastor agricolae* Marshall (1896) and *M. difficilis* Marshall (1896), described from New Zealand, similarly belong to the higher Cecidomyiinae.

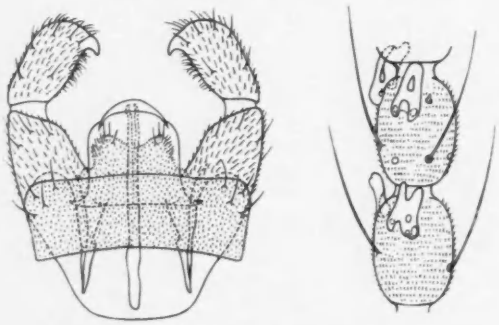

FIG. 6.—*Miastor metraloas:* dorsal aspect of hypopygium (Nisswa, Minnesota) and fourth and fifth flagellar segments of female (Stillwater, Minnesota).

Miastor metraloas Meinert

(Fig. 6)

Miastor metraloas Meinert 1865a: 37; Meinert 1865b: 83; Winnertz 1870: 7.

Miastor hospes Winnertz 1870: 6. NEW SYNONYMY.

Miastor subterraneus Karsch 1887: 200; Rübsaamen 1892: 403. NEW SYNONYMY.

Miastor americana Felt 1907: 5; Felt 1908a: 286; Felt 1911c: 82; Felt 1913: 205; Felt 1958: 90. Monotype, female, Highland, New York, June 18, 1907, in the Felt collection. NEW SYNONYMY.

Miastor hastatus Kieffer 1898: 54 (nomen nudum); Kieffer 1913a: 53; Kieffer 1913b: 313; Edwards 1941: 2. NEW SYNONYMY.

Miastor similis Kieffer 1913a: 54. NEW SYNONYMY.

Peromiastor dryobius Kieffer 1913a: 54; Kieffer 1913b: 312. NEW SYNONYMY.

None of the descriptions of the names here listed in synonymy includes characters that can be regarded as significant for species differentiation.

Felt recorded this species from Highland, Tivoli, Nassau, and Lake Placid, New York, breeding under decaying bark of maple, oak, birch, beech, and hickory. He also recorded larvae from Connecticut and Indiana.

In addition to Felt's specimens, I have studied adults from Brookwood, Surrey, England, December 31, 1944 (M. J. D. White); Lincoln, England, July 8, 1955 (R. Gair); Askeby, Denmark, May 3, 1948 (identified as *Miastor metraloas* by S. L. Tuxen); Wilton, Connecticut, September 12, 1935; Nisswa, Minnesota, July 8, 1941 (A. E. Pritchard); Frontenac, Minnesota, May 29, 1941 (A. E. Pritchard); Itasca Park, Minnesota, July 7, 1941 (A. E. Pritchard); Stillwater, Minnesota, September 6, 1941 (A. E. Pritchard); and larvae from Morris Co., New Jersey, July 3, 1940 (R. T. Weber), breeding in elm stump.

8. **Acoenoniini,** new tribe

The row of short, stout, distoventral spines on the tibia is distinctive of the tribe Acoenoniini, as is the massive genital rod of the male. The female is unknown.

Head globose. Eyes widely confluent dorsally but widely divided laterally. Ocelli three, large. Palpus with three segments, the first bearing sensory rods. Antenna of male with 2+12 segments, the flagellar segments each with a distal stem, the enlargement bearing a whorl of long sensory setae, shorter sensory setae distally, and a few short setae proximally on the more proximal segments. Legs with microchaetae and numerous tactile setae; tibia with six short ventrodistal spines; tarsus with five segments; claws gently curved, with an obtuse angulation medially; empodium rudimentary. Wing with membrane bearing microtrichia only; costa tapering beyond R_5 and without a break in the margin; h absent; Sc absent; R_s forming a right angle with R; R_5 reaching C well before end of wing; M_{3+4} absent; Cu forked near middle; PCu united with Cu; Pl absent. Hypopygium with ninth tergum nearly membranous; tenth tergites well developed; genital rod massive.

The tribe Acoenoniini is based on a single genus and species, *Acoenonia perissa* Pritchard (1947), collected in Minnesota. The female is unknown.

9. Tribe **Micromyini** Rondani

MICROMYNA Rondani 1856: 198.

MICROMYINI Pritchard 1947: 9.

CAMPYLOMYZIDES Kieffer 1898: 48.

CAMPYLOMYZARIAE Kieffer 1901: 451; Kertész 1902: 4; Felt 1908b: 311; Felt 1911a: 32; Felt 1913: 153; Kieffer 1913b: 287; Felt 1918: 297; Felt 1925: 136; Felt 1931: 425; Mani 1935: 383; Mani 1946: 189.

CAMPYLOMYZINI Enderlein 1911: 195; Enderlein 1912: 262: Edwards 1938: 173.

CAMPYLOMYZINAE Enderlein 1912: 262; Enderlein 1936: 60.

TERMITOMASTIDAE Silvestri 1901: 1; Silvestri 1903: 183.

TERMITOMASTINAE Speiser 1906: 716; Brues and Melander 1932: 274 and 348; Mani 1946: 190.

The tribe Micromyini may be recognized by the scale-like macrotrichiae on the wings and the

numerous, often scale-like, setae on the legs. The male flagellum bears one or more crenulate whorls of sensory setae, and the female flagellum usually bears sensory processes.

Head globular, the postoccipitals long. Eyes well developed laterally and with a dorsal bridge with or without dorsal or else lateral facets. Ocelli three. Palpus with one to four segments, the first with sensory rods. Antenna with 2+7 to more than 25 segments; flagellar segments of male usually with distal necks, the proximal enlargement of each with aproximal whorl of tactile setae, sometimes accompanied by sensory setae, one or more crenulate whorls of sensory setae, and distal sensory setae or processes; flagellar segments of female ovate or with distal necks, with a proximal whorl of tactile setae and with distal sensory setae or processes, the latter sometimes multipored and sometimes circumfilar. Wing membrane with macrotrichia; C ending at tip of R_5 or between tips of R_5 and M, and the margin there interrupted; h absent; Sc free; R_1 short or long; R_s present; R_5 reaching end of wing; M simple, often faint; Cu forked near its middle; CuP fused with Cu; P1 absent. Tibia without distal spines; tarsi with setae often scalelike; claws and empodium variously developed. Hypopygium with genital rod present or absent. Pigmented spermathecae two, one, or none.

Subfamily **Cecidomyiinae** Rondani, 1840

Tribe **Leptosynini** Enderlein

LEPTOSYNINAE Enderlein 1936: 64.

The tribe Leptosynini is here recognized for those paedogenic genera having five tarsal segments of which the first is shorter than the second.

Eyes with a dorsal bridge, three facets wide mediodorsally or very narrow and without facets. Ocelli absent. Palpus with one to four segments. Antenna with 2+9 to 11 segments; male flagellar segments each with a proximal whorl of tactile setae and distal sensory setae; female flagellar segments each with a proximal whorl of tactile setae and a distal sensory collar, circumfilum, or a pair of sensory processes. Wing narrow on large proximal part; membrane with erect microtrichia and with or without long and decumbent macrotrichia; Sc present or indistinct; R_1 present; R_s and M present or absent; R_5 present, sometimes evanescent distally; M_{1+2} and M_{3+4} absent; Cu simple, sometimes evanescent at end; PCu and P1 absent. Tarsus with second segment two to four times length of first; claws simple; empodium short. Hypopygium with ninth tergite well developed, the anal segment small and hidden; genital rod absent. Female abdomen with lamellae two segmented, fused or articulated to tenth tergum; sclerotized spermathecae present or absent.

KEY TO GENERA

1. Palpus with one or two segments 2
   Palpus with four segments or else three with first segment compound . . . . . **Brittenia**
2. Palpus with two segments; female with lamellae of ovipositor distinctly articulated to tenth abdominal tergite . . . . . **Frirenia**
   Palpus with one segment; female with lamellae of ovipositor fused with tenth abdominal tergite . . . 3
3. Wing membrane with macrotrichia absent or present only at distal end; female with a pair of slender sensory processes on each flagellar segment; sclerotized spermathecae present . . . . . **Leptosyna**
   Wing membrane covered with macrotrichia; female flagellar segments each with a circumfilum; sclerotized spermathecae absent . . . . . **Barnesina**

Genus **Brittenia** Edwards

Brittenia Edwards 1941: 2. Type of genus: *Brittenia fraxinicola* Edwards; monobasic and by original designation.

The genus *Brittenia* contains a single species, *B. fraxinicola* Edwards (1941), of which only females are known. In this sex the flagellar segments each bear a distal sensory collar beyond which are several small, club-shaped sensoria. The eyes are contiguous dorsally; the wing membrane bears macrotrichia; and sclerotized spermathecae are present.

Genus **Leptosyna** Kieffer

Leptosyna Kieffer 1894: 201; Felt 1911a: 37; Felt 1911c: 85; Felt 1913: 215; Kieffer 1913b: 316. Type of genus: *Leptosyna acutipennis* Kieffer; monobasic.

The genus *Leptosyna* is known only from Europe where three species are recognized: *L. nervosa* (Winnertz) 1852 (= *L. setipennis* Edwards 1919); *L. acutipennis* Kieffer 1894, and *L. quercus* Kieffer 1904. Neither of Kieffer's species has been recognized since originally described. Differences between the species, according to Kieffer, involve characters such as the comparative lengths of the stems of the male flagellum, the presence or absence of macrotrichia on the wing membrane, the slenderness of the tibia and tarsus, and the relative lengths of the tarsal segments.

I have studied a female of *Leptosyna nervosa* (a cotype of *setipennis*).

Genus **Frirenia** Kieffer

Frirenia Kieffer 1894: 201; Felt 1911a: 37; Felt 1911c: 85; Felt 1913: 216; Kieffer 1913b: 315. Type of genus: *Frirenia tenella* Kieffer; monobasic.

The genus *Frirenia* is known only from Kieffer's descriptions of *F. tenella* Kieffer (1894, 1913), on a basis of specimens reared in Bitsch. Kieffer did not describe sensoria on the female flagellum nor mention the presence or absence of spermathecae. The wing membrane was described as having microtrichia only, and Kieffer emphasized the three-segmented condition of the lamellae of the ovipositor. The male was described as having a narrow eye bridge dorsally, which is absent in the female. The palpus has two segments.

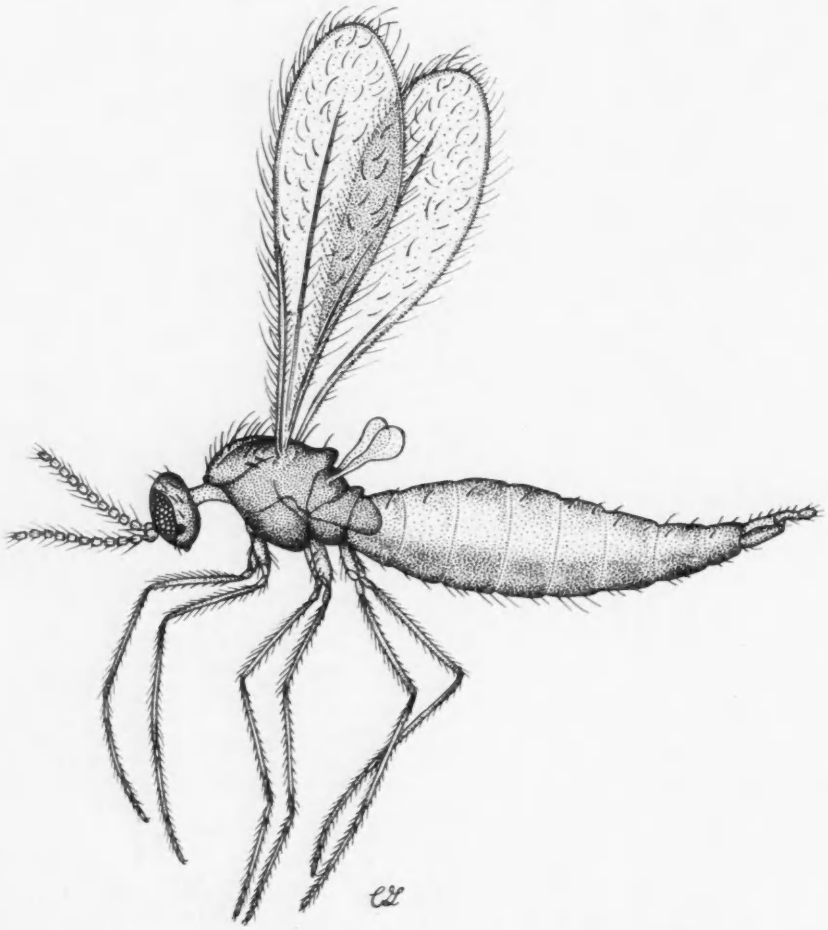

FIG. 7.—*Barnesina hylecoites:* lateral aspect of female (paratype).

Barnesina, new genus

Type of genus: *Barnesina hylecoites*, new species.

The genus *Barnesina* is closely allied to *Frirenia* Kieffer from which it differs in having the wing membrane clothed with macrotrichia, the palpus one-segmented, and the female abdomen with the tenth segment short, its tergite fused with the lamellae and capable of retraction under the ninth tergite. The flagellar sensoria of the female flagellum are unique, forming a distal circumfilum on each segment and each ring with a pair of slender projections. The disticlasper does not bear a terminal cusp as in *Leptosyna* and *Frirenia*, but may bear a brush of bristles. Sclerotized spermathecae are absent.

Head orbicular, with a pigment spot just behind each eye. Eyes with dorsal bridge present but very narrow and devoid of facets. Ocelli absent. Palpus with one segment bearing microchaetae only. Antenna of male with 2+10 or 11 segments; flagellar segments elliptical with slight distal necks, each segment with a proximal whorl of tactile setae and with long sensory setae distally. Antenna of female with 2+9 or 10 segments, the flagellar segments each with a proximal whorl of tactile setae and an irregular distal circumfilum bearing a pair of elongate projections. Legs with microchaetae and numerous long setae; basitarsus one-half to one-fourth length of second segment; claws slightly curved, simple or toothed; empodium short. Wings with microtrichia and curved macrotrichia over most of membrane and along R, R_1, R_5 and Cu; R_5 evanescent distally; R_s and base of M faint or absent; Cu simple and evanescent at tip. Hypopygium with ninth tergite well developed,

the anal segment small and hidden; disticlasper with only setae or a terminal brush; genital rod absent. Female with lamellae of ovipositor fused with tenth abdominal tergum; sclerotized spermathecae absent.

This genus is named in honor of Dr. H. F. Barnes, Rothamsted Experiment Station, Harpenden, Herts, England.

Barnesina includes two North American species. *Frirenia eocinica* Meunier (1904), described from Baltic amber, possibly belongs to this genus.

KEY TO SPECIES

1. Tarsus with second segment **2½** times length of first; disticlasper with a distal brush; ninth abdominal segment of female broader than long.... **quercivora**

   Tarsus with second segment four times length of first; disticlasper without a distal brush; ninth abdominal segment of female longer than broad.. **hylecoites**

Barnesina quercivora (Felt), new combination

Leptosyna quercus Felt 1911b: 546 (not *L. quercus* Kieffer 1904).

Leptosyna quercivora Felt 1912: 123; Felt 1958: 91. New name for *L. quercus* Felt nec Kieffer.

Leptosyna quercicola Kieffer 1913a: 54. New name for *L. quercus* Felt nec Kieffer.

Leptosyna americana Felt 1913: 216; Felt 1958: 91. NEW SYNONYMY.

Felt differentiated *Leptosyna americana* from *L. quercivora* (=*quercus* Felt) on a basis of the comparative proportions of the last two antennal segments. However, the monotype male of *L. americana* agrees in every respect with the monotype male of *L. quercivora*. The distal two flagellar segments are laterally collapsed in the type of *L. quercivora*, making only an apparent difference. Felt's 1913 figures of the antennal segments and wing are actually of the type of *L. americana*, not *L. quercivora*.

A female collected at Afton, Minnesota, September 6, 1941 (A. E. Pritchard) is regarded as being conspecific with Felt's males of *quercivora*. The eye bridge is similarly very fine and devoid of facets, the wings are similar in venation and vestitute, and the tarsi are similar. The nine-segmented flagellum of this female is very similar to that of *Barnesina hylecoites*, each segment having a proximal whorl of tactile setae and a distal circumfilum bearing two elongate projections. However, the ovipositor of *quercivora* is short and broad, and the basitarsus is longer in proportion to the second tarsal segment.

Barnesina hylecoites, new species
(Figs. 7, 8)

Barnesina hylecoites is closely allied to *B. quercivora*, differing in having the second tarsal segment four times as long as the first, the antenna of both sexes with an additional segment, the disticlasper of the hypopygium without a terminal brush, and the slender ninth abdominal segment forming the ovipositor.

MALE.—Flagellum with 10 segments, the 10th compound, the others elliptical, about twice as long as broad and with a slight distal stem, with a sparse whorl of long setae proximally and long, irregularly placed setae on more distal tubercles. Tarsus with proximal segment one-fourth as long as second segment; claw simple. Hypopygium with caudolateral angles of 10th tergite produced and bearing a dense patch of short, stout spines; disticlasper plump, with scattered setae; phallosome slender and spatulate. Length of wing 0.9 mm.

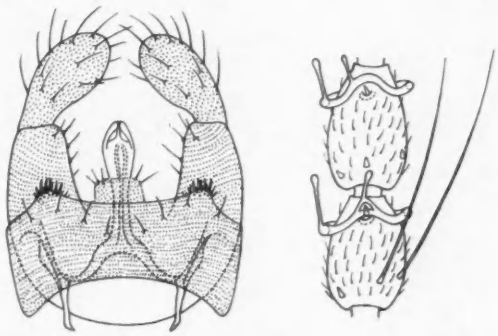

FIG. 8.—*Barnesina hylecoites*: dorsal aspect of hypopygium (holotype) and fourth and fifth flagellar segments of female (paratype).

FEMALE.—Flagellum with 10 segments, the last compound, the others obovate, about 1½ times as long as broad and with a slight distal neck, bearing a sparse whorl of proximal setae and distally with an irregular circumfilum bearing a pair of slender projections and with a pair of sensory cones. Claw with a long proximal tooth. Ninth abdominal segment much longer than broad. Length of wing 0.9 mm.

HOLOTYPE.—Male, Berkeley, California, January 14, 1952 (J. W. MacSwain), reared from rotten log; in the Pritchard collection.

PARATYPES.—Three males, 12 females, January 14, 1952 (J. W. MacSwain), reared from rotten log; 1 male, 15 females, Oakland, California, February 4, 1952 (W. C. Bentinck).

The presence of a few large eggs in the abdomen indicates that this species is paedogenic, and this was confirmed by laboratory observations of Mr. Bentinck.

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THE SEED BUGS: A CONTRIBUTION TO THE FEEDING HABITS OF THE LYGAEIDAE (HEMIPTERA: HETEROPTERA)[1]

MERRILL H. SWEET[2]

ABSTRACT

Evidence from laboratory rearings and a study of the literature indicate that the members of the large subfamily Megalonotinae are seed feeders, rather than predaceous as was commonly believed. Of the 35 species recorded from Connecticut, 33 have been studied. All have either been reared through the life cycle upon sunflower seeds and water alone, or, in a few cases where a diapause factor was involved, lived for at least 5 months on this diet. The predominance of seed feeding in the Lygaeidae is summarized. As a good, descriptive common name is lacking, the name seed bugs is here proposed for the family.

This paper discusses primarily the feeding habits of the subfamily Megalonotinae, which taxon contains nearly half of the known species of Lygaeidae. This subfamily is very widely distributed and many species are common, but biologically the subfamily is very poorly understood. Because most species of the Megalonotinae have strongly incrassate, usually stoutly-spined fore femora, authors often have surmised that the members of the subfamily are predaceous (Uhler 1876, Blatchley 1895, 1926, Butler 1923, Barber 1923).

Several references in the literature, however, have stated, indicated, or inferred that at least some megalonotine species are phytophagous. The most important of these for the present discussion is that of Ashlock (1958), who cited prior evidence of seed feeding and general phytophagy and who reared species of *Plinthisus* and *Peritrechus* from eggs to adults and observed seed feeding in other megalonotines. He concluded, therefore, that most species of this taxon subsist upon fallen seeds.

Additional evidence in the literature toward phytophagy in the Megalonotine may be mentioned. (1) *Myodocha serripes* (Oliv.) has impressed several workers with its predaceous appearance. Blatchley (1926) compared it to the carabid beetle *Casnonia pennsylvanica* (L.) and surmised that the long, slender "necks" of both species had developed through reaching into crevices in search of prey. However, *M. serripes* was found to injure strawberries (Bryson 1939); and Neiswander (1944) reared it from egg to adult upon this fruit, and even discussed methods of control. In the southern United States several other megalonotines have been reported as injurious to strawberries and as feeding on various other plants. Species of *Pachybrachius* and *Paromius* are involved here.

(2) *Pachybrachius vinctus* (Say) was recorded from strawberries in Florida by Quaintance (1897), Watson (1931), and Watson and Tissot (1942). In Puerto Rico, Wolcott (1936) reported this species upon *Hibiscus* sp., *Crotalaria* sp., and grasses, and (1950) upon *Piriqueta cistoides* (L.) Meyer and on seed capsules of *Portulaca oleracea* L. *Pachybrachius bilobatus* (Say) also was reported as feeding on strawberries by McAtee (1927), Watson (1931), and Watson and Tissot (1942); and Wolcott (1936) listed it as feeding upon cotton (*Gossypium* sp.), *Portulaca oleracea*, *Piriqueta cistoides*, milkweed (*Asclepias* sp.), and *Crotalaria* sp.

Blatchley (1926) thought the forms illustrated as *P. vinctus* by Quaintance were actually *Pachybrachius basalis* (Dallas), but McAtee (1927) stated that the figures obviously were of *P. bilobatus* (Say). Dr. Hussey (personal communication) has informed me that the two specimens of *Pachybrachius* dating from Quaintance's time now in the Florida Agricultural Experiment Station collection had been correctly identified as *P. vinctus*, but both were collected 2 years after the appearance of Quaintance's paper. However, since Quaintance described his *P. vinctus* as having a two-fold size range, he probably had both *vinctus* and *bilobatus* before him but did not differentiate them. Dr. L. C. Kuitert, of the Florida Agricultural Experiment Station, has recently done some further work on strawberry lygaeids. He found *Pachybrachius bilobatus* to be the most common of them, and reared this species to the last nymphal instar upon strawberry fruits. Dr. Kuitert has kindly permitted me to include this information, transmitted through Dr. Hussey, in the present paper.

(3) *Paromius longulus* (Dallas) was found injurious to strawberries by Watson (1931), Fletcher (1939), and Watson and Tissot (1942). Lobdell (1939) listed it as feeding upon Mexican clover (*Richardia scabra* L.), beggar-weed (probably *Bidens* sp.), Bermuda grass (*Cynodon dactylon* (L.)), *Crotalaria* sp., Jew-grass (?), mai-

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Just recently, after this paper had gone to press, translations of important papers by Puchkov (1956) and Putshkova (1956) have become available, in which, among other biological information, seed feeding in the Lygaeidae is discussed.

den cane (*Panicum hemitomon* Schult.), St. Augustine grass (*Stenotophrum secundatum* (Walt.)), *Lilium longiflorum* Thunb., amaryllis (*Atamasco atamasco* (L.)), and gladiolus (*Herbertia* sp.). He also described distinct migrations from strawberries to other plants and vice versa, and attributed this behavior to water needs. Douglas and Ingram (1942) reported *Paromius longulus* as a minor pest, though common to abundant, in the rice fields of Louisiana and Texas; like the more important rice stink bug, *Oebalus* (=*Solubea*) *pugnax* (Fabr.), it punctured the kernels, leaving circular spots, and caused a condition known as "pecky rice."

(4) In Senegal and Nigeria, groundnuts (peanuts), either unshelled or shelled and stored, have been fed upon by the megalonotines *Rhyparochromus sordidus* (Fabr.) (Roubaud 1916, Risbec 1941, Mackie 1944, Howe 1952, and Cotterell 1952), *Aphanus apicalis* Dallas (Roubaud 1916, Risbec 1941), and *Dieuches armipes* (Fabr.) (Roubaud 1916). (5) *Aphanus sordidus* (Fabr.) was detected feeding on benniseed (*Sesamum orientale* L.) by Cotterell (1952). (6) *Dieuches annalatus* Sign. was found living on castor bean plants in Madagascar (Frappa 1931). (7) Cobben (1953), in Holland, recorded *Trapezonotus arenarius* (L.) as feeding on seeds of *Erodium circutarium* L'Hérit.

The foregoing records show that the literature contains positive evidence of specific phytophagy —not mere collections of chance specimens from plants (records of which are rife in the literature) which, without observed feeding, can not constitute host-plant records. However, when a species occurs in large numbers on a given plant, definite feeding association is likely.

In June 1957 I began an intensive study of the ecology and bionomics of the members of the Megalonotinae of Connecticut. I can now state conclusively not only that these insects are not predaceous, but that they subsist primarily, if not exclusively, upon the seeds of various plants. First, to test the question of predatism, I repeatedly attempted to induce many species, such as *Ozophora picturata* Uhler, *Myodocha serripes* (Oliv.), and *Cnemodus mavartius* (Say), to feed upon aphids, mealworms, small caterpillars, beetles, Collembola, mites, and sowbugs. The lygaeids made no attempt to feed upon any of the arthropods, and died in a short time. By contrast, out of the 35 species in 27 genera recorded from Connecticut, 33 species in 27 genera were either reared through the entire life cycle or, in a few cases where a diapause factor was involved, lived for at least 5 months in the fall and winter upon hulled sunflower seed and water alone.

The rearing method was simple. Petri dishes of 4-inch outside diameter were used as rearing containers. Water was provided in narrow-necked 1-ounce vials, stoppered with cotton. Despite a lack of environmental controls, this arrangement proved generally successful for small, laboratory populations of megalonotines. Probably, however, the resulting moderately high humidity, but low actual moisture, resembled the sublitter microhabitat preferences of most species, despite the rather striking habitat differences of the individual species. These conditions protected the eggs of many species from drying. Some, as *Stygnocoris rusticus* (Fallén), *S. pedestris* (Fallén), *Drymus unus* (Say), and *Carpilis consimilis* Barber, laid their eggs upon and in the moist cotton stopper. Others, as *Cryphula parallelogramma* Stal, *Xestocoris nitens* Van Duzee, *Sisamnes clavigera* (Uhler), and *Ozophora picturata* Uhler, laid eggs upon a dry substrate; but, in order to hatch, the eggs required high humidities, at least during early development. A ring of vaseline served well to keep out pests (especially mites) and to keep the small first-instar nymphs inside the petri dish halves.

When water in vials was readily available the megalonotines fed but sparingly upon such herbaceous materials as lettuce, grass, etc., whereas seeds were vigorously fed upon. Sunflower seeds (*Helianthus annuus* L.) were adopted for laboratory use as they were acceptable to all species, apparently provided an adequate diet, were large, and easily available. They were hulled to provide easier feeding.

Recently collected adults and nymphs, when introduced into containers with sunflower seeds, usually began to feed within minutes, and some, for example *Peritrechus* sp., *Scolopostethus diffidens* Horv., and *Ligyrocoris diffusus* Uhl. pushed and flailed with legs and antennae, apparently vying for possession of a seed. Only with adults of *Sphragisticus nebulosus* (F.), and *Xestocoris nitens* V.D. was there appreciable mortality in the transition from field food and conditions to laboratory food. Nymphs of all instars could be taken from the field and easily reared through to the adult stage despite the obvious shift in food material.

In rearing nymphs from the eggs a heavy mortality usually occurred in the first instar, but the remainder usually developed normally. Nymphs reared individually showed the same sort of mortality, especially in continuous rearing. This mortality was very marked in *Scolopostethus diffidens*, *Eremocoris ferus*, *Megalonotus chiragra* (F.), and *Perigenes constrictus* (Say), among others. *Cnemodus mavortius*, *Peritrechus* sp., and *Antillocoris minutus* Bergr. showed a much higher percentage of survival, and *Sisamnes clavigera*, a low mortality.

The reason for this mortality is not known, but it might be anticipated when one considers the radical change in conditions from the field to the laboratory including being fed a seed which is exotic to Connecticut. *Scolopostethus diffidens* Horv. suffered a mortality of over 90% upon sunflower seeds but significantly enough, when

the seeds of *Betula populifolia* L., the gray birch, were provided, a much lower mortality resulted. First-instar nymphs that failed to survive upon a diet of sunflower seeds and water alone were observed to feed on sunflower seeds and usually lived until the time of the first moult or longer but then died.

Sunflower seeds are evidently a rich food. Two or three seeds kept a half-dozen adults alive and well for a month or more, depending on the species, or provided enough nourishment to allow three or four nymphs of such larger species as of *Zeridoneus* or *Ligyrocoris* to complete development. According to Hurt (1946) the sunflower seed is composed typically of 46% oils which contain oleic, linolic, and palmitic fatty acids. Unlike most oil seeds, they are high in protein with 30%, very low in water with 7% or less, 5% cellulose, 7% carbohydrates, and 5% ash. The seed kernels are high in vitamin B, but deficient in phosphates and potash. This deficiency may be related to the mortality.

Despite the xeric habitats which many of the species frequent, water of metabolism was not adequate for any of the 33 species; on the contrary, an ample water supply was needed. In nature, water is presumably obtained from plants, dew, and ground moisture. Under petri dish conditions, the seeds ordinarily became moldy quickly, but under heavy feeding such molds were either greatly reduced or eliminated. Under such heavy feeding the seeds were reduced to shriveled husks. It was noted that the seed became softer and oilier after a few days of feeding.

The adaptability of the Megalonotinae to the laboratory should make them favorable material for experimental work, as two other lygaeids of another subfamily, *Lygaeus kalmii* Stal and *Oncopeltus fasciatus* (Dall.) have become.

Because of their ground-living habits it is difficult to acquire direct field evidence of feeding upon seeds. A few species, however, have been observed occasionally to climb up into plants to feed on seeds. *Ligyrocoris diffusus* has often been observed feeding upon the seed heads of the black-eyed susan (*Rudbeckia hirta* L.) sometimes with as many as 10 insects clustered on a head. In the laboratory they fed on these same seeds by holding them individually with their fore tarsi. *Stygnocoris pedestris* and *S. rusticus* have both been observed in nature feeding upon the seeds of the bitter-buttons (*Tanacetum vulgare* L.). Many other seeds from various microhabitats have been tested with different species in the laboratory. A more comprehensive analysis of these results will be developed in a later contribution to the ecology of these insects.

The alacrity with which the various species of megalonotines fed upon a seed which is not indigenous to the study area, and the ease and success of feeding, suggest that most of the species are at least potentially polyphagous or oligophagous upon seeds. This also means that in habitat selection, host plant preferences are likely to be of lesser importance than edaphic factors. This is a problem that requires specific analysis. For example, *Megalonotus chiragra* was found by Slater and Sweet (1958) to feed readily upon sunflower seeds but showed a definite field preference for the seeds of bachelor's buttons (*Centaurea cyanus* L.). It is noteworthy that *Centaurea*, like *M. chiragra*, is a European immigrant.

In the family Lygaeidae, seed feeding has been recorded in scattered references from other subfamilies as well as the Megalonotinae. More definite records exist, for many of the species occur upon the plant itself, where they may be readily observed. Even so, the portion of the plant fed upon is usually not recorded. Nevertheless, as Ashlock (1958) noted, Hoffman (1932), in his review of the economic status of the family, recorded seed feeding in a number of lygaeids.

While it should be emphasized that nothing is known of the feeding habits of the great majority of the lygaeid species, a few examples from different subfamilies should suffice to show the importance and widespread occurrence of seed feeding. In the Lygaeinae, the milkweed bugs, *Oncopeltus fasciatus* and *Lygaeus kalmii*, bred readily on only milkweed seeds and water (Andre 1932, Simanton and Andre 1936). In the Orsillinae, *Belonochilus numenius* (Say) completed its life cycle upon the seed balls of the sycamore tree (*Platanus occidentalis* L.) (Heidemann 1902, Van Duzee 1914). The members of the Cyminae have nearly always been taken from the seed heads of the Cyperaceae (sedges and bullrushes) (Slater 1952). *Kleidocerys resedae* (Panz.) of the Ischnorrychinae has been well studied. It was found by Claassen (1922) to subsist upon the dry overwintered seeds of the cat-tail (*Typha* sp.) and by Jordan (1933) upon the dry seeds of birch (*Betula* sp.). In the Pachygronthinae, *Oedancala dorsalis* (Say) feeds upon sedge seeds (Van Duzee 1888) and *Phlegyas abbreviatus* (Uhler) upon grass seeds (Slater 1951). In the Oxycareninae, many species of *Oxycarenus*, especially *hyalinipennis* Costa, feed on cotton seeds (*Gossypium hirsutum* L.) (Kirkpatrick 1923), and upon other malvaceous plants such as *Sida* sp. and *Hibiscus* sp. (Odhiambo 1957). Seed-feeding very likely occurs in the Heterogastrinae, as Dicker (1943) found 500 nymphs and a few adults of *Heterogaster urticae* (L.) clustered at the tips of two heads of nettles and none elsewhere. In the Artheneinae, *Chilacis typhae* Perr. is well known in Europe to feed upon the overwintered seeds of the cat-tail (*Typha* sp.) (Douglas and Scott 1865, Butler 1923, et al.). Nothing yet is known of the feeding habits of the small subfamilies Pamphantinae, Malcinae, Bledionotinae, and the Slaterellinae.

While phytophagous, several subfamilies are exceptions in that seed feeding is not recorded. The Blissinae and the small subfamily Chauliopinae apparently feed regularly upon the sap of the host plants. In the latter subfamily, *Chaulops rutherfordi* Dist. was described by Golding (1937) as feeding in Nigeria upon the leaves of *Calopogonium mucunoides* and *Desmodium mauritiamum*, and a related species is a pest of beans in Japan. The Blissinae are commonly found to feed upon the sap from the bases of grass plants, as does the chinch bug, *Blissus leucopterus* Say.

This leaves only the Geocorinae as known to be definitely predaceous. At least one species of the Cleradini (in Megalonotinae), *Clerada apicicornis* Sign. is definitely hematophagous (Costa Lima 1940). Others have been found in mammal nests, and Corrêa (1956) considered the group as important vectors of *Trypanosoma* in South America. About the small subfamily Henesterinae, which is closely related to the Geocorinae, little is known, but they may very well share the habits of the geocorines. I have found that *Geocoris ulighinosus* (Say), *G. bullatus* (Say), and *Hypogeocoris piceus* (Say), while actively predaceous upon small insects in the laboratory (in contrast with the megalonotines), are by no means obligate predators, for all three species survived upon sunflower seeds and water, without evident discomfort, for as long as 3 or 4 months. Moreover, they fed on the seeds in the presence of potential prey. This apparent omnivorousness may well account for the high abundance of many of the geocorines, which has always puzzled students who have considered them strictly predatory. In view of the prevalence of seed feeding, it is very likely that the Geocorinae and the Cleradini are derived from seed feeding ancestral forms.

As Mayr et al. (1953, p. 51) stressed, the family concept usually has a biological as well as a morphological unity. The various species of a family may occupy similar habitats or possess similar habits. This biological unity is often expressed in the common name used for the family as "carrion beetles" for the Silphidae, "hover flies" for the Syrphidae, or "plant bugs" for the Miridae. The Lygaeidae lack such a descriptive name and have often been called the "chinch bug family" because of the destructiveness of the chinch bug, *Blissus leucopterus*, upon small grains and corn in central North America. From the foregoing discussion it is apparent that seed feeding is a very wide spread habit in the Lygaeidae, occuring in both ground living and plant living species, and in most of the subfamilies. Seed feeding, then, is the generalized and characteristic feeding habit. Thus, I venture to suggest that an appropriate and satisfying name for the Lygaeidae would be *the seed bugs*.

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PREDATORY MITES OF THE FAMILY CUNAXIDAE ASSOCIATED WITH CITRUS IN FLORIDA[1]

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ABSTRACT

Six species of *Cunaxa* and two of *Cunaxoides*, most of them uncommon to rare, are recorded, and a key to them is given. *Cunaxoides* **pectinellus** is a new species.

While investigating the factors that contribute to the natural control of insects and mites injurious to citrus in Florida, a number of species of predatory mites have been identified. As expected, several proved to be undescribed so a series of descriptive studies was initiated to make valid names available for biological control investigations and discussions. The first of these studies was concerned with mites of the family Phytoseiidae and was published in 1955.[2] The present paper is the second of the series.

Mites of the family Cunaxidae, with the excep-

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[2]Muma, Martin H. 1955. Phytoseiidae (Acarina) associated with citrus in Florida. Ann. Ent. Soc. America 48(4): 262–72.

tion of one species, *Cunaxa taurus* Kramer, are uncommon to rare on citrus. Eight species are recorded; three occur only in the litter under the trees, two on the limbs and trunks, one on the leaves, and two in the litter and on the leaves. Two genera are represented, *Cunaxa* von. Heyden and *Cunaxoides* Baker and Hoffman. Analyses and notes on the species are given below.

The mites were mounted in a chloral hydrate medium and examined under magnifications varying from 125× to 500× with phase contrast illumination. Measurements of the one new species were made under 125× magnification and corrected to the nearest 0.01 mm.

All recorded collections were made by the author unless otherwise noted.

The type of the new species is deposited in the mite collections at the United States National Museum in Washington, D. C. Acknowledgements are due Dr. Edward W. Baker of that museum for assistance in the identification of material and for criticism of the manuscript.

Family Cunaxidae Thor

These mites are small to moderate sized, with elongate pyriform bodies. The integument is soft and finely striated, with a suture between the propodosoma and hysterosoma. The gnathosoma is long and cone-like, with raptorial palpi and elongate, weakly-chelate chelicerae. Leg tarsi bear claws and pulvilli. The propodosoma bears four elongate, sensory setae. Dorsal scuta and two pairs of genital suckers are usually present.

The following key is designed only for those species of cunaxids that are known to be associated with citrus in Florida. Generic separations are valid only for the species included in this paper.

KEY TO THE CUNAXIDAE ASSOCIATED WITH CITRUS IN FLORIDA

1. Palpi five-segmented and much longer than chelicerae ..... **Cunaxa** von Heyden . 2
   Palpi three-segmented and scarcely longer than chelicerae ..... **Cunaxoides** B. and H . 6
2. Dorsal scutum divided into four scuta as shown in figure 1; palpus with a large process between the tibia and tarsus ..... **Cunaxa taurus** (Kramer)
   Dorsal scutum transversely divided into two scuta; palpus without a mesal process between tibia and tarsus but with a distinct femoral process 3
   Dorsal scutum entire; palpus without either a mesal process between the tibia and tarsus or a femoral process 4
3. Femoral process on palpus large and flange-like **Cunaxa capreolus** (Berlese)
   Femoral process on palpus small and spur-like **Cunaxa womersleyi** Baker and Hoffman
4. Palpus with a process on the mesal surface of the tarsus but no strong spine on the tibia ..... **Cunaxa simplex** (Ewing)
   Palpus with no process on the mesal surface of the tarsus but strong spines on the tibia and tarsus 5
5. Palpus with a strong mesal spine on the patella **Cunaxa setirostris** (Hermann)
   Palpus with no strong mesal spine on the patella .. **Cunaxa boneti** B. and H.
6. Tarsus of the palpus with two small processes ..... **Cunaxoides andrei** B. and H.
   Tarsus of the palpus with one large process ..... **Cunaxoides pectinellus,** new species

Genus **Cunaxa** von Heyden

Cunaxa von Heyden 1826, Isis (Oken) 18: 609.

Cunaxids possessing five-segmented palpi that are much longer than the chelicerae but are not provided dorsally or ectally with a modified spine or spur.

Type species: *Cunaxa setirostris* Hermann, 1804.

Cunaxa taurus (Kramer)

Figures 1, 8, and 13

Scirus taurus Kramer 1881, Zeitschr. ges. Naturwiss. 54: 433–5, 19. 3, figs. 9–11.

Cunaxa taurus, Sig Thor 1912, Zool. Anz. 39: 389; Baker and Hoffman 1948, An Escuela Nac. Cienc. Biol. México 5: 232, figs. 6–8.

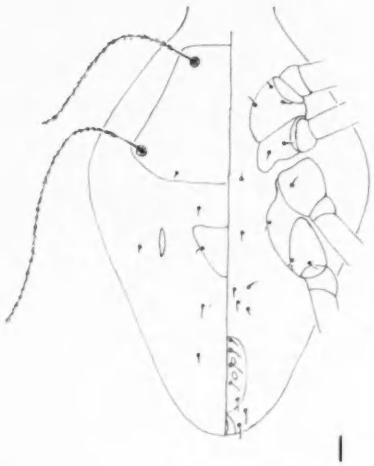
This species is characterized by four reticulate dorsal scuta. The palpus has a large mesal process between the tibia and tarsus, at least one strong mesal spine on both the tibia and tarsus and a slender spur-like, mesal, femoral process.

Records: Highlands Hammock State Park, Sebring, one female on sour orange leaf, February 15, 1953. Bamboo, Whitney, one female on orange leaf, March 25, 1952; one female, September 12, 1952; one female on orange leaf, January 9, 1953; one female, November 19, 1953. Yalaha, one female on scaly orange leaf, November 19, 1952. Weirsdale, four females in litter under citrus, November 20, 1958 (H. L. Greene). Palm Harbor, one female on citrus leaf, January 30, 1952 (K. Townsend); one male, February 13, 1952 (K. Townsend). Brooksville, one male on tangerine leaf, October 14, 1952 (K. Townsend). Ft. Pierce, one male on orange leaf, December 16, 1958 (H. L. Greene).

Remarks: This relatively common cunaxid is found occasionally in some numbers in certain groves. Although the normal coloration of the species is red, both green and brown individuals have been collected. The species occurs on the trees and in the litter beneath the trees.

EXPLANATION OF PLATE I

Dorsal and ventral scuta and spination. FIG. 1.—*Cunaxa taurus* (Kramer). FIG. 2.—*C. capreolus* (Berlese). FIG. 3.—*C. womersleyi* Baker and Hoffman. FIG. 4.—*C. setirostris* (Hermann). FIG. 5.—*C. simplex* (Ewing). FIG. 6.—*Cunaxoides andrei* Baker and Hoffman. FIG. 7.—*C. pectinellus* new species.



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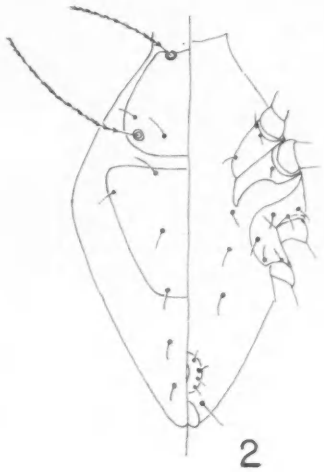

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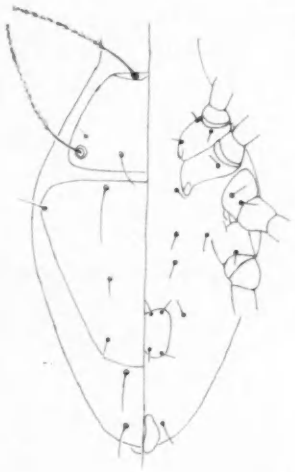

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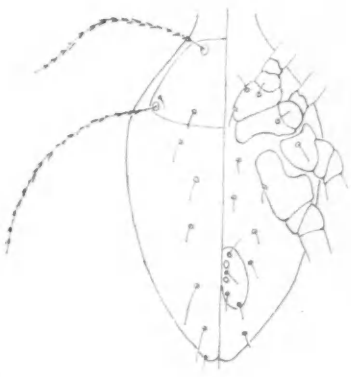

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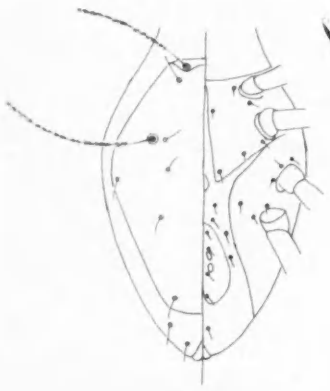

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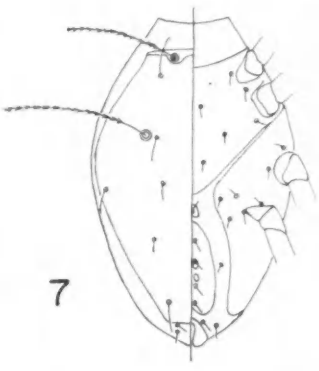

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Cunaxa capreolus (Berlese)

Figures 2, 9, and 20

Scirus capreolus Berlese 1890, Acari, Myriapoda et Scorpiones hucusque in Italia reperta, Fasc. 57, No. 9.
Cunaxa capreolus, Vitzthum 1929, Tierwelt Mitteleuropas 3(3): 60; Baker and Hoffman 1948, An. Escuela Nac. Cienc. Biol. México 5: 231–2, figs. 1–5.

This species has the dorsal scutum divided transversely into two smooth scuta. The palpus has a strong mesal spine on both the tibia and tarsus and a flange-like, mesal, femoral process.

Records: Oak Hill, one male on twig from *Citrus sinensis* May 22, 1953 (L. C. Knorr).

Remarks: Only one specimen of this species has been collected.

Cunaxa womersleyi Baker and Hoffman

Figures 3, 10, and 17

Cunaxa womersleyi Baker and Hoffman 1948, An. Escuela Nac. Cienc. Biol. México 5: 234–5, figs. 9–10.

This species is characterized by a transversely divided, smooth, dorsal scutum. The palpus has a strong mesal spine on both the tibia and tarsus and a small spur-like, mesal, femoral process.

Records: Weirsdale, many males, females, and nymphs from litter beneath orange trees, November 20, 1958 (H. L. Greene and M. H. Muma).

Remarks: This species was abundant in the single collection, but must be considered rare.

Cunaxa simplex (Ewing)

Figures 5, 11, and 14

Scirus simplex Ewing 1917, Bull. Amer. Mus. Nat. Hist. 37: 150–1, pl. 1, fig. 21.
Cunaxa simplex, Sig Thor and Willmann 1941, Das Tierreich 71: 173–2; Baker and Hoffman 1948, An. Escuela Nac. Cienc. Biol. México 5: 240–1, figs. 31–39.

This species is characterized by the lack of strong spines on the tibia of the palpus, and by a single small tubercular process on the mesal surface of the tarsus. The dorsal scutum is punctate and undivided, and the coxal scuta for legs 1 and 2 are fused.

Records: Lake Alfred, one female in litter under citrus tree, July 21, 1952.

Remarks: This species is apparently uncommon in citrus groves as only one record has been obtained.

Cunaxa setirostris (Hermann)

Figures 4, 12, and 21

Scirus setirostris Hermann 1804, Mémoire Aptérologique, p. 62, pl. 3, fig. 12.
Cunaxa setirostris, von Heyden 1926, Isis (Oken) 18: 609; Baker and Hoffman 1948, An. Escuela Nac. Cienc. Biol. México 5: 237–8, figs. 23–25.

The species is identified by a lightly punctate, undivided dorsal scutum, no mesal process on the tarsus of the palpus, and strong spines on the mesal surface of the patella, tibia, and tarsus of the palpus.

Records: Archer, one female on purple scale-infested orange leaf, November 21, 1958 (A. G. Selhime).

Remarks: The collection of a single specimen indicates that this species is rare on citrus foliage.

Cunaxa boneti Baker and Hoffman

Cunaxa boneti Baker and Hoffman 1948, An. Escuela Nac. Cienc. Biol. México 5: 237, fig. 22.

This species has the dorsal scutum undivided, no process on the mesal surface of the tarsus of the palpus, and strong spines present mesally on only the tibia and tarsus of the palpus.

Records: Oak Hill, one nymph on twig of *Citrus sinensis*, May 23, 1953 (L. C. Knorr).

Remarks: This species is not illustrated as no adults have been taken from citrus.

Genus **Cunaxoides** Baker and Hoffman

Eupalus Koch 1838, Deutschlands Crustaceen, Myriapoden und Arachniden, Fasc. 20, fig. 21. (Not *Eupalus* Gistel 1834.)
Cunaxoides Baker and Hoffman 1948, An. Escuela Nac. Cienc. Biol. México 5: 241.

Cunaxids with three-segmented palpi that are scarcely longer than the chelicerae.

Type species: *Cunaxoides croceus* (Koch 1838).

Cunaxoides andrei Baker and Hoffman

Figures 6, 16, and 18

Cunaxoides andrei Baker and Hoffman 1948, An. Escuela Nac. Cienc. Biol. México 5: 249–50, figs. 60–68.

This species is characterized by the presence of a finely punctate dorsal scutum provided with six pairs of setae in addition to the sensory setae, two processes on the tarsus of the palpus, and three slender spatulate sensory setae on the tarsus of the first leg.

Records: Lake Alfred, two females and one nymph from litter under grapefruit tree, July 17, 1952. Weirsdale, four females from litter under orange trees, January 15, 1953 (M. H. Muma and J. A. Coddington). Bluefields, one female from citrus leaf, November 15, 1958.

Remarks: This species exhibits some variation in ventral sclerites and spination.

Cunaxoides pectinellus, new species

Figures 7, 15, and 19

Female holotype 482 μ long and 237 μ wide. Leg 1 = 230 μ, 2 = 214 μ, 3 = 230 μ, and 4 = 252 μ.

EXPLANATION OF PLATE II

Armature of distal ends of palpi and second legs. FIGS. 8 and 13.—*Cunaxa taurus* (Kramer). FIGS. 9 and 20.—*C. capreolus* (Berlese). FIGS. 10 and 17.—*C. womersleyi* Baker and Hoffman. FIGS. 11 and 14.—*C. simplex* (Ewing). FIGS. 12 and 21.—*C. setirostris* (Hermann). FIGS. 16 and 18.—*Cunaxoides andrei* Baker and Hoffman. FIGS. 15 and 19.—*C. pectinellus* new species.

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This species is closely related to *C. pectinatus* (Ewing) from which it may be distinguished by a larger, more quadrate tarsal apophysis on the palpus, differences in the setal armature of the ventral coxal sclerites, the position of the para-anal setae, and spination of the dorsal scutum, which is punctate and undivided.

Records: Known only from the holotype collected from litter under citrus trees at Bamboo (Whitney), Florida, December 17, 1952. Holotype deposited in the United States National Museum in Washington, D. C.

NOTES ON THE ENTOMOLOGICAL WRITINGS OF ASA FITCH, M.D., WITH SPECIAL REFERENCE TO HIS CATALOGUES AND REPORTS[1]

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ABSTRACT

The Entomological writings of Asa Fitch, the journals in which they appeared, and their unavailability are discussed briefly. Attention is called to errors in references to those of his publications that contain descriptions of new genera and species. Complete citations are given to the orginal and subsequent printings of the papers that contain the descriptions of most of the Fitch genera and species.

Asa Fitch began publishing on entomological matters as early as 1845, and between that date and 1872 when his last contribution appeared, he authored at least 118 papers. Most of his writings appeared in agricultural periodicals, such as the American Agriculturist, the Cultivator, the Genesee Farmer, and the Country Gentleman, the last being his publishing medium for 58 articles. Other studies were published in the American Quarterly Journal of Agriculture and Science, and most of the remainder appeared in journals financed by the State of New York, including the Journal of the New York State Agricultural Society, Transactions of the New York State Agricultural Society, and the Annual Report of the Regents of the University [of the State of New York]. Dr. Fitch's works covered the entomological field of his time and are of general interest, but they are of special concern to taxonomic entomologists for they contain descriptions of numerous new genera and species.

Although Fitch articles are frequently referred to in present-day literature, his writings apparently are not generally available. Indeed, they seem to have been scarce soon after his death in 1879, for J. A. Lintner, who was entomologist to the State of New York during much of the last quarter of the 19th century, often mentioned the unavailability and importance of the Fitch publications. In a paper dealing with Fitch and his work, Lintner (Entomological Reports of Dr. Asa Fitch. *In:* Appendix to First Annual Report on the Injurious and Other Insects of the State of New York 1883 (1882), pp. [291]–325) gave an annotated list of the 14 "Reports" and 103 additional papers. Although Lintner stated that his list was incomplete, it doubtless contains nearly all titles and especially those that are of major importance. It consequently is of value to persons concerned with the work of Dr. Fitch. At the present time, however, this article apparently is nearly as difficult to obtain as are the Fitch publications themselves.

It is evident from perusal of the Fitch publications, as well as from Lintner's annotated list, that in many cases identical articles were published in more than one place and in different years, and that the pagination differed in each case. This duplication has resulted in numerous inconsistencies and much confusion in Fitch citations, for in general, subsequent workers seem to have been unaware of the situation and have cited any date and page known to them even though it may not have been the earliest one. It seems desirable, therefore, to present information designed to make it possible for workers to cease perpetuating the errors that have existed. To this end complete references are here given to one "Catalogue" and to the 14 "Reports", since these publications contain the descriptions of nearly all of Fitch's genera and species, and also to subsequent printings of these papers.

Fitch published two "Catalogues," but only the one cited here contained descriptions of new species or descriptive material.

1851. Catalogue with References and Descriptions of the Insects Collected and Arranged for the State Cabinet of Natural History. *In:* Fourth Annual Report of the Regents of the University, on the Condition of the State Cabinet of Natural History, and the Historical and Antiquarian Collection annexed thereto. Made to the Senate, January 14, 1851. 4: [43]–69. [Homoptera only].

This work was republished by Lintner who stated (p. [381]):

"In this reprint, it is designed to reproduce the

[1]Accepted for publication September 11, 1959.

paper in its original form, *litteratum et punctuatum*, with the exception of the introduction in the text of the small reference figures, indicating corrections in the names, or notes thereon given in supplementary pages. The paging of the Fourth Report is retained in the catalogue, in brackets.

"In compliance with request, Mr. E. P. Van Duzee, of the Grosvenor Library, Buffalo, N. Y., has kindly made revision of the nomenclature of the Catalogue as far as the Psyllidae, and indicated such changes therein as are accepted at the present time. The remainder of the catalogue, comprising the Psyllidae, Aphididae, and Coccidae, has been revised and annotated by Dr. C. V. Riley. The names in the catalogue unaccompanied with the reference figures are unchanged."

Lintner's citation follows:

1893. Catalogue of the Known Homoptera of the state of New York in 1851. *In:* Appendix to Report of the State Entomologist for the year 1892. New York State Museum, Forty-sixth Annual Report of the Regents for the year 1892, pp. [381]–413. [Fitch's "Catalogue" appears on pages 383–409, and the "Corrections and Notes" by Van Duzee and Riley occupy pages 410–413.]

Fitch's 14 "Reports" were first published in the Transactions of the New York State Agricultural Society, and the first 11 were also published separately. The titles of the "Reports" varied slightly and they are here given in full, with the citations as published in the Transactions, and also as they appeared in the separates. The original "Reports," with the exception of the 13th and 14th, as well as the separates, most of which were issued later than the originals, were printed by Van Benthuysen, Albany, printer to the New York State Legislature. The same type was used for the text of both printings, but some reprints contain an index that was absent from the original, and plates that appeared in two of the original "Reports" were omitted from the reprints, or at least are not present in the reprints that I have examined.

REPORTS IN THE TRANSACTIONS OF THE NEW YORK STATE AGRICULTURAL SOCIETY

1855. Report [on the Noxious, Beneficial and Other Insects, of the State of New York.] (1854) 14: [705]–[880], text figs.

1856. Report on the Noxious, Beneficial and Other Insects, of the State of New York. (1855) 15: [409]–559, text figs., 4 pls.

1856. Third Report on the Noxious and Other Insects of the State of New York. (1856) 16: [315]–490, text figs., 4 pls.

1858. Fourth Report on the Noxious and Other Insects of the State of New York. (1857) 17: [687]–[753], text figs.

1859. Fifth Report on the Noxious and Other Insects of the State of New York. (1858) 18: [781]–854, text figs.

1861. Sixth Report on the Noxious and Other Insects of the State of New York. (1860) 20: [745]–868, 2 pls.

1862. Seventh Report on the Noxious and Other Insects of the State of New York. (1861) 21: [813]–859, 1 pl. [Includes explanation of plates in Sixth and Seventh Reports.]

1863. Eight Report on the Noxious and Other Insects of the State of New York. (1862) 22: [657]–691, text figs.

1864. Ninth Report on the Noxious and Other Insects of the State of New York. (1863) 23: 778–823, text figs., 1 pl.

1865. Tenth Report on the Noxious and Other Insects of the State of New York. (1864) 24: 433–461, text figs.,1 pl.

1867. Eleventh Report on the Noxious, Beneficial and Other Insects of the State of New York. (1866) 26: 487–543, text figs.

1868. Twelfth Report on the Noxious, Beneficial and Other Insects, of the State of New York. (1867) 27 (pt. 2): 889–932.

1870. Thirteenth Report on the Noxious, Beneficial and Other Insects of the State of New York. (1869) 29: [495]–566.

1872. Fourteenth Report on the Noxious, Beneficial and Other Insects of the State of New York. (1870) 30: 355–381.

The 11 reports published separately appeared as follows:

"1855. First Report on the Noxious, Beneficial and Other Insects, of the State of New York, . . . , pp. 180, Including Index." [Quoted from Lintner (p. 294).]

1856. First and Second Report on the Noxious, Beneficial and Other Insects, of the State of New York. [Under this title page the reports are as follows:]
Report of Asa Fitch, M.D., on the Noxious, Beneficial, and Other Insects of the State of New York. 1–[176] pp., text figs.
Report on the Noxious, Beneficial and Other Insects, of the State of New York. [177]–336 pp., text figs., 4 pls. [Includes an index to the two reports.]

1859. Third, Fourth, and Fifth Reports on the Noxious, Beneficial and Other Insects, of the State of New York.
[Under this title page the reports are as follows:]
Third Report on the Noxious and Other Insects of the State of New York. [III]–VII, [3]–172 pp., text fig. [Contains no plates as did the original report.]
Fourth Report on the Noxious and Other Insects of the State of New York. 1–67 pp., text figs.
Fifth Report on the Noxious and Other Insects of the State of New York. [1]–74 pp., text figs. [Has 11 unnumbered pages of index to the three reports.]
A note preceding the index states, "These three reports . . . are paged separately—the printer having supposed they were to form three pamphlets instead of one volume."

1865. Sixth Report on the Noxious and Other Insects of the State of New York. [3]–126 pp., 2 pls.
Seventh Report on the Noxious and Other Insects of the State of New York. [127]-173 pp., 1 pl. [Includes explanation of plates in Sixth and Seventh Reports.]
Eight Report on the Noxious and Other Insects of the State of New York. [175]–209 pp., text figs.
Ninth Report on the Noxious and Other Insects of the State of New York. [211]–[260] pp., text figs., 1 pl. [Includes an index to Sixth, Seventh, Eighth and Ninth Reports.]

1867. Tenth Report on the Noxious and Other Insects of the State of New York. 1–29 pp., text figs. [Contains no plate as did the original report.]
Eleventh Report on the Noxious, Beneficial and Other Insects of the State of New York. [31]–90 pp., text figs. [Includes an index to Tenth and Eleventh Reports.]

LAPHYSTIA LOEW IN NORTH AMERICA (DIPTERA: ASILIDAE)[1]

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ABSTRACT

This and three related genera are keyed. In *Laphystia* 29 species are recognized from the Nearctic Region and northern Mexico. These are arranged in nine species groups and are included in a key. *L. albiceps* (Macq.), of doubtful status, is not so treated. Twelve species are new: *L.* **brookmani,** *L.* **cazieri,** *L.* **howlandi,** *L.* **jamesi,** and *L.* **martini** (California); *L.* **sonora** (Mexico); *L.* **duncani** (Arizona); *L.* **utahensis** (Utah); *L.* **tolandi** (Nevada and Utah); *L.* **laguna** (Texas); *L.* **bromleyi** (Oklahoma and Arkansas); and *L.* **snowi** (Kansas).

Fifty years ago the genus *Laphystia* Loew was known by four species in America north of Mexico (Back 1909). Curran (1927, 1931) added eight species, and clarified the status of some of those previously described. James (1941) described a species from Colorado and gave notes on two described species. Hull (1958) described two species from Arizona and one from California. In the present paper 12 species are described as new, and notes and descriptions are given for some of those known previously.[2] Unless otherwise stated, the types of the new species will be deposited in the California Academy of Sciences.

The position of *Laphystia* Loew and related genera in the Asilidae has been in question for many years. Williston (1884) included *Laphystia* Loew and *Triclis* Loew in the subfamily Dasypogoninae, as did Back (1909), but both considered them intermediate between the Dasypogoninae and Laphrinae. Williston (1891) included *Triclis* in the Dasypogoninae and *Laphystia* in the Laphrinae. Hermann (1920) proposed the subgroup Pyrtaniinae for *Laphystia* and related genera and included them in the Dasypogoninae. This classification was followed by Brues and Melander (1932). Bromley (1932) changed it to the tribe Pyrtaniini. Hardy (1948) included *Laphystia* in the tribe Laphystiini and remarked that as Hermann's names were not based upon generic ones, they must ultimately disappear from classifications. Carrera (1950) divided the Brazilian Dasypogoninae (which includes the subfamily Laphrinae) into seven tribes, one of which is Laphystiini; the genera included were *Triclioscelis* Roeder, *Macahyba* Carrera, *Apoxyria* Schiner, *Laphystia* Loew, *Psilocurus* Loew, and *Triclis* Loew.

According to Engel (1930), *Laphystia* Loew is represented in the Palearctic region by six species, including the genotype *sabulicola* Loew. Only one specimen of *sabulicola* has been seen, and from this meagre evidence it appears to be congeneric with the Nearctic species. *Laphystia* Loew has been reported from the Neotropical Region by Williston (1891), Curran (1931), and Carrera (1950), but no authentic species are known to me.

These flies are found on the sandy beaches of streams, lakes, and oceans, and on saline or alkaline flats near or adjacent thereto. It is anticipated that many more species will be found as other areas are explored.

Laphystia Loew can be separated from the remainder of the Asilidae by the following combination of characters. Head about 1½ times as broad as high; width of face at antennae subequal to that of one eye, facial gibbosity extending from oral margin to base of antennae, the antennae situated on its posterior declivity; first antennal joint broader and slightly longer than second, third slightly club-shaped, its length subequal to that of the first two combined; style short, broad, two-jointed, concave apically and with an apical spine, frons not much wider at vertex than at antennae; palpi with two segments. Dorsocentral bristles absent; marginal cell of wings closed and sometimes short-petiolate, costa extending to sixth longitudinal vein (Cu_1 and Cu_2), margin of axillary cell and axillary lobe membranous, fourth posterior cell closed and petiolate, first posterior cell usually open but sometimes closed and petiolate, vein R_4 S-shaped. Femora not greatly larger than their tibiae; fore tibiae without a twisted apical spine or spur; pulvilli present, but greatly reduced in some species. Abdomen short and broad, with lateral bristles on segments 1 to 6; male with six and female with eight visible segments; female terminalia without articulating spine.

Engel (1930) gave a key to the Palearctic genera, several of which had not been recognized by

[1]Accepted for publication September 18, 1959.
[2]The following persons supplied specimens or assisted in other ways: Paul H. Arnaud, Jr., Entomology Research Division, A.R.S., U.S.D.A.; the late R. H. Beamer, University of Kansas; the late S. W. Bromley, Stamford, Conn.; Bernard Brookman, U.S. Public Health Service; Owen Bryant, Montara, Calif.; J. F. Gates Clarke, U.S. National Museum; C. H. Curran, American Museum of Natural History; D. K. Duncan, Globe, Ariz.; the late C. T. Greene, of the former Bureau of Entomology and Plant Quarantine, U.S.D.A.; M. T. James, Washington State College; C. Don MacNeill, California Academy of Sciences; Charles H. Martin and H. A. Scullen, Oregon State College; A. Earl Pritchard, University of California; (Berkeley); Bernard Rotger, C. R., Gardner, Colo.; and G. Stuart Walley, Entomological Branch, Department of Agriculture, Ottawa, Canada.

Séguy (1927), and Carrera (1950) keyed the Brazilian genera. The most important characters for separating *Laphystia* from related genera are: the broad, gibbous face, short antennae, membranous margin of the axillary cell and lobe, femora not greatly larger than their tibiae and and without spines, abdomen with lateral bristles on segments 1 to 6. This and allied Nearctic genera can be separated by the following key.

1. Face subequal to width of one eye, in profile evenly swollen from oral margin to base of antennae; abdomen with lateral bristles on segments 1 to 6; wing margin of axillary cell and lobe membranous, costa ending at sixth longitudinal vein (Cu_1 and Cu_2); first posterior cell usually open, sometimes closed ..... **Laphystia** Loew
   Face at antennae not more than two-thirds as wide as one eye, in profile at most the lower two-thirds gibbous 2
2. Face at antennae one-half as wide as one eye, in profile the lower one-half or less swollen; abdomen with lateral bristles on segments 1 to 6; first posterior cell broadly open; costa extending completely around wing ..... **Psilocurus** Loew
   Face at antennae two-thirds as wide as one eye; abdomen at most with lateral bristles on segments 1 and 2; first posterior cell closed and petiolate ... 3
3. Face in profile most prominent at oral margin, gradually receding to the middle; mystax composed of a single row of oral bristles and dense, recumbent hairs above; lateral bristles on abdominal segment 1 only; diameter of hind femora about 1⅓ times that of their tibiae ..... **Perasis** Hermann
   Face in profile swollen on the lower two-thirds, most prominent at the lower one-third; mystax composed of numerous bristle-like hairs over the entire gibbosity; lateral bristles on abdominal segments 1 and 2; diameter of hind femora twice the greatest diameter of their tibiae ..... **Zabrops** Hull

Zabrops Hull (1958b) was erected for *Triclis tagax* Williston and related species, from the United States. *Triclis argentifacies* Williston, from Mexico, does not belong in the genus *Triclis* Loew; from the figures and description given by Engel (1930) it can be better placed in *Perasis* Hermann, at least temporarily. *Perasis* Hermann is known from four species in the Palearctic Region, and *sareptana* Hermann, from Sarepta, is its genotype.

Curran (1927, 1931) and James (1941) described the male abdomen of *Laphystia* Loew as having seven visible segments. From the works of Young (1921), Cole (1927), and Crampton (1942), it seems evident that what they considered the first abdominal segment is the epimeron of the metathorax. In this paper only six segments are considered to be visibly present in the male abdomen (exclusive of the terminalia), each of which bears lateral bristles. The first two segments have four or more lateral bristles, and the number usually decreases caudad so that segments 5 and 6 may have only one or two.

Examination of freshly collected male specimens of *Laphystia jamesi*, new species, shows that segments 7 and 8 are completely hidden by the sixth segment and are largely membranous, with the sternal terga wholly so. The chitinized portion of the seventh tergum dorsally is about one-sixth as long as the sixth tergum, and laterally is expanded caudad into a rounded lobe bearing four or five short hairs and one longer hair directed posteriorly; these lobes are about one-third the length of the sixth tergum. The eighth tergum is rounded dorsally at the middle, and is about one-seventh as long as the sixth tergum; laterally it is narrow, about one-twelfth the length of the sixth. The genitalia are small and rounded, and largely concealed by the sixth tergum. The hypandrium, or ninth sternum, is about one-half as long as the sixth sternum, slightly rounded anteriorly and broadly pointed apically, with a posterior fringe of sparse hairs.

There are eight visible segments in the female abdomen, exclusive of the terminalia. Segments 1 to 6 are similar to those of the male, but segments 7 and 8 are very short and sometimes are not evident from above.

The species can be arranged in groups, as follows.

A. Pollinose fasciae entire on abdominal segment 1 or 2, or on both:
   B. Scutellum with dense, long, erect hairs over the entire disc: **opaca group** (*opaca, litoralis, texensis, laguna*).
   BB. Scutellum with short, recumbent discal hairs:
      C. Scutellum with long marginal hairs or bristles:
         D. Scutellum with marginal bristles; fasciae on abdominal segment 6 narrowly interrupted: **sexfasciata group** (*sexfasciata, limatula, tolandi*).
         DD. Scutellum with marginal hairs; fasciae on abdominal segment 6 entire:
            E. Segment 2 of abdomen almost wholly pollinose: **howlandi group** (*howlandi, utahensis*).
            EE. Segment 2 of abdomen pollinose only on posterior margin: **flavipes group** (*flavipes, annulata, torpida, snowii, brookmani, cazieri*).
      CC. Scutellum without long marginal hairs or bristles:
         F. First posterior cell of wings open: **confusa group** (*confusa, rufofasciata, lanhami, rubra*).
         FF. First posterior cell of wings closed and petiolate: **martini group** (*martini*).

AA. Fasciae on abdominal segments 1 to 5 interrupted:
   G. Scutellum entirely pollinose: **notata group** (*notata, canadensis, ochreifrons, varipes, bromleyi*).
   GG. Scutellum not entirely pollinose:
      H. Scutellum with only the narrow posterior margin bare of pollen; fasciae on abdominal segment 6 broadly interrupted: **rufiventris group** (*rufiventris*).
      HH. Scutellum with disc largely bare, sometimes with posterior margin also bare; fasciae on abdominal segment 6 entire: **jamesi group** (*jamesi, duncani, sonora*).

KEY TO THE SPECIES

1. Abdominal segment 1 or 2, or both, with the pollinose fasciae entire or nearly so, or these segments wholly or largely pollinose[3] 2
   Abdominal segments 1 to 5 with the pollinose fasciae broadly interrupted 21
2. Entire disc of scutellum clothed with dense, erect hairs, as long as first two antennal segments, which cannot be differentiated from marginal hairs or bristles; face at antennae 1⅙ times as wide as one eye 3
   Disc of scutellum clothed with recumbent hairs, with or without longer marginal hairs or bristles; face at antennae subequal to or narrower than width of one eye 6
3. Fasciae on all abdominal segments entire 4
   Fasciae on abdominal segments 3 to 5 interrupted .. 5
4. Abdominal segments 3 to 6 each with a black, transverse, pollen-free triangle in middle near base; length 8 to 10 mm. (Tex., La.) ..... **opaca**
   Abdominal segments 3 to 6 with basal half shining black, except laterally; length 9 to 12 mm. (Tex., La.) ..... **texensis**
5. Legs black, tips of femora and not more than basal one-fourth of tibiae yellowish; wings hyaline; style of antennae about one-third as long as third joint; length 10 to 12 mm. (N. Y., Fla., Ga., N. C., N. J., Va.) ..... **litoralis**
   Basal half of tibiae and hind femora, and basal one-sixth and one-third of fore and middle femora, respectively, yellowish; wings infuscated; style of antennae one-half as long as third joint; length 9 to 11 mm. (Tex.) ..... **laguna**
6. Scutellum with longer marginal hairs or bristles 7
   Scutellum with short, recumbent hairs only 17
7. Scutellum with marginal bristles (as strong as lateral bristles on mesonotum); fasciae on abdominal segments 4 to 6 usually narrowly interrupted 8
   Scutellum with marginal hairs; fasciae on abdominal segment 6 entire 10
8. Abdomen wholly reddish, basally somewhat darker; basal half or more of femora yellowish; pulvilli four-fifths as long as claws;[4] length 9 to 12 mm. (N. Mex., Ariz.) ..... **limatula**
   Abdomen black or dark brownish; femora usually with more black 9
9. Femora black, narrowly reddish at base and apex, tibiae black; scutellum with four marginal bristles; pulvilli three-fifths as long as claws; abdomen dark brown; length 9 to 10 mm. (Nev., Utah) ..... **tolandi**
   At least basal one-fourth of fore and middle femora and basal half of hind femora reddish; basal half of tibia reddish; six or more marginal bristles on scutellum; pulvilli four-fifths as long as claws; abdomen black; length 9 to 12 mm. (Mo., Kans., Nebr.) ..... **sexfasciata**
10. Segment 2 of abdomen almost wholly pollinose; scutellum with sparse, erect, discal hairs 11
    At most the posterior margin of abdominal segment 2 pollinose; scutellum with recumbent discal hairs 12
11. Abdomen wholly yellowish, fasciae on segments 3 to 5 one-third the length of the segments; femora of both sexes wholly yellowish; second and third antennal joints reddish; pulvilli two-thirds as long as claws; length 8 to 9 mm. (Utah) ..... **utahensis**
    Abdomen yellowish-red, fasciae on segments 3 to 6 one-half the length of segments; apical one-fourth of fore and middle femora, and entire dorsum of hind femora, black; antennae black; pulvilli three-fifths as long as claws; length 8 to 9 mm. (Calif.) ..... **howlandi**
12. Pulvilli subequal in length to claws 13
    Pulvilli at most two-thirds as long as claws 15
13. Femora yellow, at most the tips of fore femora black above; fasciae on abdominal segments 3 to 5 one-half the length of segments; length 8 mm. (Ariz.) ..... **annulata**
    Apical half or more of male and at least tips of female femora black; fasciae on abdominal segments 3 to 5 at most two-sevenths the length of segments 14
14. Basal one-fourth of fore femora and basal three-fourths of middle and hind femora yellowish in males; mesonotal and abdominal hairs white; fasciae on segments 1 to 6 entire and equal to two-sevenths length of segments; length 8 to 9 mm. (Mont., Wyo., Nebr., Minn., Manitoba) .. **flavipes**
    Basal one-half of fore femora and basal three-fourths of middle and hind femora yellowish in males; recumbent mesonotal and abdominal hairs golden; fasciae on segments 3 to 5 interrupted, equal in width to one-sixth length of segments; length 8 mm. (Kans.) ..... **snowii**
15. Fasciae on first abdominal segment broadly interrupted, on segments 2 to 6 entire; pulvilli one-half as long as claws; abdomen and legs brown, base of tibiae yellowish; length 8 mm. (Calif.) .. **torpida**
    Fasciae on segments 1 to 6 entire; pulvilli two-thirds as long as claws 16
16. Abdominal segments 1 and 2 largely pollinose; scutellum with about 15 marginal hairs; length 9 to 11 mm. (Calif.) ..... **cazieri**
    Fasciae on abdominal segments 1 and 2 narrow; scutellum with about 24 marginal hairs; length 9 to 11 mm. (Calif.) ..... **brookmani**
17. First posterior cell closed and petiolate; abdomen wholly brown or yellowish-brown and almost wholly pollinose; pulvilli one-fourth as long as claws; length 8 to 10 mm. (Calif.) ..... **martini**
    First posterior cell broadly open; basal half of most segments bare of pollen; pulvilli and claws subequal in length 18
18. Abdomen wholly reddish-brown; femora black on dorsal surface; length 8 mm. (Ariz., Colo.) .. **rubra**
    Abdomen black, at most, reddish under the pollinose fasciae 19
19. Femora wholly yellow; tibiae yellow except at tips; fasciae on segments 4 and 5 broadly interrupted, that on segment 3 sometimes interrupted; mesonotal hairs very short, recumbent, golden; length 8 to 10 mm. (Okla., Wyo., Tex.) ..... **confusa**
    Fore femora at least largely black on dorsal surface. 20
20. Fasciae very narrowly interrupted on segment 4, interrupted by about one-fourth width of abdomen on segment 5; abdomen reddish under the pollinose fasciae; length 8 to 9 mm. (Wyo., Colo.) ..... **rufofasciata**
    Fasciae on segments 4 and 5 broadly interrupted in both sexes; no reddish color under pollinose fasciae; length 8 to 9 mm. (Colo.) ..... **lanhami**
21. Scutellum entirely pollinose 22
    Scutellum with disc in part, or narrow posterior margin, or both, bare of pollen 26
22. Basal one-fifth, or less, of hind femora yellowish or reddish 23
    Basal one-third, or more, of hind femora yellowish. 24

[3]Abdominal segment 1 is the first segment to bear lateral bristles.

[4]Claws and pulvilli are measured from the base of the claws, and the ones used are those of the hind legs.

23. Mesonotum of male largely bare of pollen, that of female with small bare spots before and behind suture on either side; frons of female ochreous; length 9 to 11 mm. (Ky., Ohio, La.) **ochreifrons**

Mesonotum of male with bare portion divided by the central pollinose stripes, that of female with bare spots behind suture only; frons of female light yellow; length 10 to 11 mm. (Manitoba, Iowa, Nebr., Kans., Mont., Wyo.) **canadensis**

24. Mesonotal hairs in both sexes as long as second antennal joint; hairs laterally on abdomen as long as first two antennal joints; central area of mesonotum largely bare of pollen; length 10 to 11 mm. (Okla., Ark.) **bromleyi**

Mesonotal hairs short and recumbent except laterally in females and behind the suture in males; longer hairs on sides of abdomen confined at most to first three segments . . . 25

25. Mesonotal hairs short and recumbent, except marginally, in both sexes; lateral hairs on abdomen short and recumbent on segments 3 to 6 in males, on 2 to 6 females; abdomen sometimes reddish under the pollinose fasciae; basal two-thirds or more of hind femora reddish; length 11 to 12 mm. (Okla., Kans., N. Mex., Tex.) **varipes**

Mesonotal hairs anterior to suture as long as first antennal segment in males, confined to dorsocentral rows in females; hairs on sides of abdomen short and recumbent on segments 4 to 6 in males, on 3 to 6 in females; abdomen and antennae black or brown; basal half or less of hind femora reddish; length 9 to 10 mm. (Tex.) **notata**

26. Scutellum with only narrow posterior margin bare of pollen; abdomen largely reddish . . . 27

Scutellum with disc largely bare of pollen, sometimes posterior margin also bare; abdomen black . . . 28

27. Legs black, very narrow apices of femora and narrow bases of tibiae yellowish; abdominal segments 4 to 6 yellowish-red, basal segments brown to black; fasciae broadly interrupted on all segment including 6; length 11 mm. (Wyo. Colo.) **rufiventris**

Femora and at least basal one-fourth of tibiae reddish-brown, dorsum of femora largely black; abdomen reddish-brown; fasciae usually entire on segments 1, 2, and 6, but sometimes indistinct on 1 and 2 and narrowly interrupted on 6; length 8 to 9 mm. (Ariz., Colo.) **rubra**

28. Posterior margin of scutellum pollinose, disc largely bare; pollen on sides of abdomen narrow; fasciae about one-third length of segments and separated at middle by one-fifth width of abdomen; femora narrowly reddish-brown at base; length 11 mm. (Mexico) **sonora**

Posterior margin of scutellum, and disc in part, bare of pollen; pollen on sides of abdomen broad . 29

29. Femora black, narrowly reddish-brown at apices; basal one-third of tibiae brown; mesonotum largely pollinose; length 9 to 12 mm. (Calif.) **jamesi**

Basal one-third or more of hind femora and basal one-half or more of tibiae reddish-brown; mesonotum largely bare of pollen; length 10 to 11 mm. (Ariz., Calif.) **duncani**

Laphystia (?) **albiceps** (Macquart)

Dasypogon albiceps Macquart 1842, Dipt. Exot., Suppl. I: 69, 51.

Laphystia albiceps, Back 1909, Trans. Amer. Ent. Soc. 35: 227.

This species was described from Texas. It is not included in this or in any of the previous keys. Its type must be examined before either its specific or its generic status can be established. Back (1909) gave a translation of the original description.

Laphystia annulata Hull

Laphystia annulata Hull 1958, Psyche 64(2): 72–73.

Types (both sexes), near Navajo, Ariz., VII–11 '54 (F. M. Hull), in the Hull collection. A female specimen, same data, which has the gray bands on the abdomen distinctly interrupted is designated as *Laphystia annulata interrupta* Hull, in the Hull collection.

Typical specimens have been seen from the following localities. ARIZONA: Beaver Dam Wash., U. S. Highway 260, VI–29 and 30, VII–1 and 20 '49, and VIII–16 '48 (C. H. and Dorothy Martin, Itol J. and J. Wilcox). UTAH: Mt. Carmel Jct., VII–11 '48 (Jean Duspiva).

The pulvilli are subequal to the claws in length. In some specimens the apical abdominal segments are brown, wholly or in part, and in some the apical two-fifths or less of the fore femora are black dorsally.

Laphystia bromleyi, new species

Male: Length 10 mm. Head black, densely white-pollinose, palpi and proboscis shining. Hairs white, mystax reaching to antennae, erect hairs on frons and ocellar tubercle as long as the first two antennal joints; occipital bristles yellowish-white. Face slightly narrower than width of one eye. First two antennal joints black, white-haired, the second narrower and three-fourths as long as the first, the first with 2 or 3 yellowish bristles below; the third brown, narrowly reddish at base, subequal in length to the first two joints; style one-fourth as long as third joint.

Mesonotum shining black; broad sides, humeri and area inside the humeri, the central stripe narrowly anteriorly, and the posterior margins narrowly, gray-pollinose. Hairs white, on the dorsum fine, semiappressed, and about as long as second antennal joint, marginal hairs about as long as the first two antennal joints. Bristles yellowish, three presutural, two or three supraalar, and two postalar. Pleurae and coxae densely gray-pollinose and white-haired. Scutellum wholly gray-pollinose, hairs white, the discal hairs semiappressed and as long as first antennal joint; about 40 marginal hairs as long as first two antennal joints.

Abdomen black, the sides and posterior margins gray-pollinose; fasciae on segment 6 entire, interrupted by from five-sixths to one-half the width of the abdomen on segments 1 to 5. Hairs on the sides white and as long as the first two antennal joints, dorsally appressed, with a yellowish cast, bristles yellowish. Genitalia black, hairs white. Venter densely gray-pollinose, hairs white, the narrow posterior margins appearing yellow under the pollen.

Legs black; fore and middle femora narrowly

reddish or yellowish at base and apex and densely white-pollinose, hind femora with the basal one-fourth reddish above and below, and on the sides about the basal one-half reddish, dorsum gray pollinose. Basal one-fourth, one-third, and one-half of the fore, middle, and hind tibiae respectively, yellowish. Hairs white, bristles yellowish-white. Apical half of claws black, basally yellowish; empodia brown; pulvilli light brown, four-fifths the length of the claws.

Halteres brown at base, knob and stem yellowish. Alulae yellowish, short hairs white. Wings hyaline, veins light brown, first posterior cell narrowed; anterior crossvein at middle of discal cell.

Female.: Length 10 mm. Similar to male. Face with a light golden cast, mystax sparse but with the long hairs reaching antennae, clump of bristles below at middle of face yellowish. Mesonotal and pleural pollen with a golden cast. Abdominal segments 7 and 8 wholly gray-pollinose, terminalia brown. Anterior crossvein at five-twelfths length of discal cell, first posterior cell slightly narrowed.

Holotype: Male, Sallisaw, Okla., VI–21 '37 (Standish-Kaiser) (S. W. Bromley Collection 1955), in the U. S. National Museum. *Allotype:* Female, same data, U.S.N.M. *Paratypes:* 1 male, 3 females, same data; 1 male, Gore, Okla., VII–20 '37 (Standish-Kaiser) (S. W. Bromley Collection 1955); 1 male, 3 females, Arkansas Co., Ark., VI–27 '27 (S. W. Bromley Collection 1955); in the U.S.N.M. and the writer's collection. One male, one female, Stillwater, Okla., V–13 '34 and VI–14 '33 (A. E. Pritchard); in the Pritchard collection.

The female specimens from Arkansas have the basal four-fifths of the hind femora and the basal two-thirds of the hind tibiae yellowish.

Laphystia brookmani, new species

Male: Length 9 mm. Head black, densely white-pollinose; hairs white; bristles white, about 12 below at middle of mystax. First antennal joint black, white-haired and with two white bristles below, wider and 1⅓ times as long as second joint; third subequal in length to first two together; style broad, about one-fourth length of third joint.

Mesonotum black, densely gray-pollinose, the broadly bisected central stripe bare of pollen anteriorly; hairs yellowish white, numerous, erect, and about as long as first antennal joint. Bristles yellowish, two presutural, three supraalar and two postalar. Pleura and coxae densely gray-pollinose and white-haired. Scutellum densely gray-pollinose, the middle two-thirds of the posterior margin black; discal hairs white, dense, semierect; marginal hairs white, about 25 in number.

Abdomen brownish black, sides and posterior margins of all segments gray-pollinose; the fasciae on the first segment narrow, about one-fourth the length of the segment and situated at three-fourths its length. Hairs short, white, longer on sides of first three segments; bristles white varying from one to five per side of each segment. Genitalia brownish black, white-haired. Venter gray-pollinose and erect white-haired.

Legs, including trochanters, brownish-black, the knees narrowly lighter brown; hairs white, bristles yellowish; claws black, basal one-third reddish; pulvilli white, two-thirds length of claws; empodia light brown.

Halteres yellow, base brown. Wings light brown, veins brown; anterior crossvein at two-fifths length of discal cell; anal cell closed at wing margin.

Female: Length 9 mm. Similar to male. Hairs on face only about half as long as in the male, subequal in length to first antennal joint. Abdominal segments 7 and 8 wholly gray-pollinose; small ovipositor brown, white-haired. Narrow base of hind femora and all tibiae reddish brown.

Holotype: Male, Middletown, Lake Co., Calif., VII–28 '40 (T. Aiken, B. Brookman, C. Michener), in the Brookman collection. *Allotype:* Female, same data, in the Brookman collection. *Paratypes:* 12 males and 16 females, same data. In some of these the narrow fasciae on the first abdominal segment is weak or almost obliterated. See note under *L. torpida*.

Laphystia canadensis Curran

Laphystia canadensis Curran 1927, Canadian Ent. 59: 87.

Holotype male and allotype female, Westbourne, Manitoba, VII–10 '26 (G. S. Brooks), and female paratype, Sioux City, Iowa, VII–3 '17 (C. N. Ainslie), in the Canadian National Collection.

A male specimen from Atchison Co., Kansas, was compared with the holotype by G. Stuart Walley and declared the same; a female from Doniphan Co., Kansas, had less red on the legs than the allotype female which, according to Mr. Walley, had the basal half of the hind femora and tibiae reddish.

Specimens have been identified from the following localities: IOWA, Sioux City, VII–4 '22 (C. N. Ainslie). KANSAS, Atchison Co., VII–11 and 14 '24 (R. H. Beamer, E. P. Breakey), Doniphan Co., VII–22 '24 (Beamer) and VIII–21 '21 (W. J. Brown), Douglas Co., VII–22 '19 (W. F. Hoffman). MONTANA, Glendive, VI–18 '30 (Ainslie), Malta VII–27 '27 E27–317, Powderville, VII–4 '16. NEBRASKA, Lincoln, VI–21 '12 (R. W. Dawson, L. M. Gates), VI–26 '36 (Bratt), VI–29 '25 (C. E. Mickel), So. Sioux City, VII–16 '12 (L. T. Williams). SOUTH DAKOTA, Elk Point, VI–19 '24, H. Pierre (collection of J. M. Aldrich). WYOMING, '81 (Morrison).

Most specimens have only the basal one-fourth or one-fifth of the hind femora reddish but, as

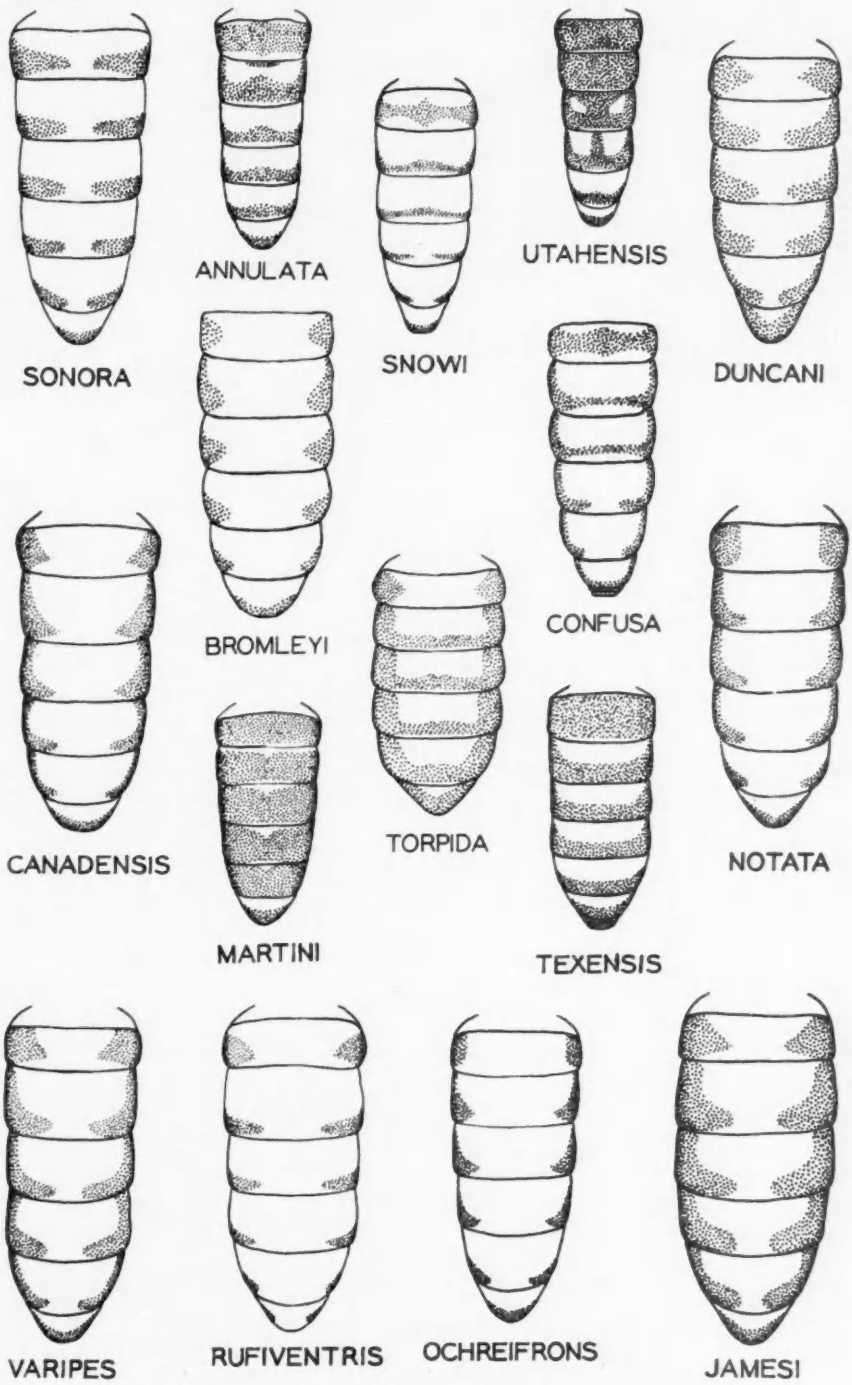

FIG. 1.—Pollinose patterns of the abdomen of *Laphystia* species. Males are illustrated, except for *L. limatula* and *L. rufofasciata*. All are drawn to the same scale. Pollinose areas are indicated by stippling.

indicated above, some of the females may have the basal one-half reddish. The fasciae are separated by about two-thirds the width of the abdomen in males and by about five-eighths in females. The pulvilli are subequal to the claws in length.

Laphystia cazieri, new species

Male: Length 9 mm. Head densely white-pollinose, palpi and proboscis black. Hairs and bristles white, mystax composed entirely of hairs as long as the first two antennal joints. Face at antennae subequal to width of one eye. Antennae black; hairs white, numerous on first, sparse on second; first with three strong white bristles below; first broader and about 1¼ times as long as second, third subequal in length to first two, style one-third as long as third.

Mesonotum gray-pollinose, bisected central stripe darker and for a short distance anteriorly shining black, dorsocentral stripes before and behind suture for a short distance and a narrow stripe on either side posteriorly, shining black. Semiappressed hairs golden, plus erect white hairs as long as first antennal joint, longer anteriorly and posteriorly. Bristles white, two presutural, two or three supraalar, and three postalar; dorsocentral hairs undifferentiated from longer hairs posteriorly. Pleurae and coxae gray-pollinose and white-haired. Scutellum gray-pollinose, posterior margin black; discal hairs appressed, white, but as long as first antennal joint; about 15 long, white, marginal hairs.

Abdomen black, sides and posterior margins of all segments gray-pollinose, the fasciae becoming narrower apically, first segment largely and the second with a narrow anterior band. Hairs white, longer on sides of first two segments, bristles white, varying from two to five per segment. Genitalia black, white-haired. Venter gray-pollinose, erect white hairs long and rather numerous. Legs black, knees very narrowly brownish, hairs and bristles white; claws black, basal one-fourth reddish; empodia brown; pulvilli white, two thirds as long as claws.

Halteres yellowish, lower stem brown; alulae yellowish, margin white. Wings light brown, veins dark brown; anterior crossvein at two-fifths length of discal cell; anal cell short petiolate.

Female: Length 11 mm. Similar to male. Abdominal segments 7 and 8 wholly pollinose. Femora narrowly brownish at base. *Holotype:* Male, Coalinga, Calif., V–14 '38 (M. Cazier), in the Brookman collection. *Allotype:* Female, same data, in the Brookman collection. *Paratype:* Two males and two females, same data.

Laphystia confusa Curran

Laphystia confusa Curran 1927, Canadian Ent. 49(4): 86–87.

Type male, Wichita National Forest, Oklahoma, VI–6 '06 (W. J. Brown), No. 2363 in the Canadian National Collection; paratype male, Wyoming, July 1905.

Female: Length 9 mm. Head black, gray-pollinose, the face and frons yellowish; hairs white, bristles yellowish, three or four below on first antennal joint and a clump of about 10 at middle of face. Scutellum gray-pollinose, narrow posterior margin shining black, disc and posterior margin with short, recumbent, golden hairs. Abdomen black, the broad sides and narrow posterior margins white-pollinose, entire on segments 1 and 2, narrowly interrupted on 3 and 6, and more broadly interrupted on 4 and 5. Femora wholly yellowish, tibiae yellowish except at apex, apex of tibiae and the tarsi brownish; pulvilli subequal to claws in length. Wings light brown, veins brown, the anterior ones yellowish.

Hypotype: Female, Selling, Okla., VI–2 '39 (Kaiser-Nailon), in the Pritchard collection.

Other specimens from the following localities: *Oklahoma:* Waurika, VII–4 '37 and Cherokee, VI–4 '37 (Standish-Kaiser). TEXAS: Forestburg, VII–11 to 20 '41 (L. H. Bridwell); and Denison, VI–24 (H. S. Barber).

The *confusa* group is characterized by the very short, recumbent hairs on the mesonotum and scutellum and on the sides and dorsum of abdominal segments 2 to 6.

Laphystia duncani, new species

Male: Length 10 mm. Head densely white-pollinose, vertex thinly so, palpi and proboscis shining black. White-haired, occipital bristles yellowish. Face subequal to width of one eye. Antennae black, first joint white-pollinose, the remainder yellowish-pollinose; first joint 1½ times length of second and broader, both white-haired, first with three pale yellowish bristles below; third subequal to length of first two together; style about one-fourth as long as third joint.

Anterior fourth of mesonotum including humeri, broad lateral and posterior margins, and postalar calli, yellowish-pollinose, the narrow suture gray-pollinose; remainder black. White hairs numerous, erect, and as long as first antennal joint. Bristles yellowish, two presutural, two or three supraalar, and two or three postalar. Pleura largely yellowish-pollinose, below and the coxae grayish, hairs white. Scutellum shining black, narrow sides gray-pollinose, recumbent discal and erect marginal hairs yellowish.

Abdomen shining black, the broad sides and posterior margins yellowish-gray-pollinose, fasciae on segment 1 broadly interrupted, on segments 2 to 5 interrupted by about one-fourth the width of the segments, entire on segment 6. Hairs white on pollinose areas and quite long on sides of first two segments; short, recumbent, and black on black areas. Lateral bristles white on segment 1, yellowish on the remainder, and varying from three to six. Genitalia shining

black, white-haired. Venter uniformly grayish-pollinose and white-haired, the narrow posterior margins yellowish.

Legs black; fore and middle femora narrowly at base and apex, basal one fourth of hind femora, yellowish-red, and all gray-pollinose; basal two-thirds of fore and middle and basal five-eighths of hind tibiae, yellowish-red; claws black, basal three-fifths reddish; pulvilli whitish, subequal to claws in length. Hairs and bristles white, long below on middle femora.

Halteres light yellow, base brown. Wings grayish hyaline, veins brown; anterior crossvein at about two-fifths length of discal cell; first posterior cell broadly open, anal cell closed, fourth posterior cell broadly truncate basally.

Female: Length 10.5 mm. Similar to male. Face and front with a yellowish tinge. Pollen of mesonotum more extensive, the central stripe divided and the area before the suture entirely pollinose except a narrow dorsocentral black spot. Abdominal fasciae slightly more widely separated on segments 1 to 5, entire on 6, segments 7 and 8 wholly pollinose; short terminalia shining black.

Holotype: Male, Tempe, Ariz., April (D. K. Duncan). *Allotype:* Female, same data. *Paratypes:* 112 specimens with the same data, and Piachaco Lake, Ariz., April (Duncan), and Pinal County, Ariz., April (Duncan); 1 male and 2 females, Ehrenberg, Ariz., IV–14 '41 (N. R. Anderson, Itol J. and J. Wilcox, Jr.). One male, Gila Bend, Ariz., IV–24 '38 (F. H. Parker), in the Pritchard collection. One female, Blythe, Riverside Co., Calif., IV–4 '51 (J. W. MacSwain), University of California (Berkeley).

Laphystia flavipes Coquillett

Laphystia flavipes Coquillett 1904, Proc. Ent. Soc. Washington 6: 180.
Laphystia flavipes Back 1909, Trans. Amer. Ent. Soc. 35: 229.
Laphystia sexfasciata, Curran 1927, Canadian Ent. 59: 85–86, and 1931, Amer. Mus. Novitates No. 487: 12 (misidentification; not Say).

Described from "Montana and North Carolina. Two males collected by H. K. Morrison. Type—No. 7950, U. S. National Museum". Paul H. Arnaud, Jr., says, "I have found only one specimen which is labeled 'Mon' 'Collection Coquillett' Type No. 7950 U.S.N.M. It is a female." Dr. Arnaud has labeled this specimen lectotype.

The specimen from North Carolina, another female, was found in the National Museum by Dr. Arnaud with the following labels: "N. C.", "Collection Coquillett", "Laphystia 6-fasciata Say" probably in Dr. Aldrich's handwriting, and a fourth label, "I doubt this N. C. label, det. A. E. Pritchard". This specimen is in poor condition, but seems to be best placed in *flavipes* with a question about the locality until similar specimens have been collected in North Carolina.

Curran has made *flavipes* a synonym of *sexfasciata* and has described specimens from Manitoba as *sexfasciata*. This procedure could be correct, but Say's description applies equally well to a species more common in "Missouri" (Nebraska and Kansas) than *flavipes*; so it seems more logical to retain both names than to erect a new one. *L. flavipes* is one of our most northern species and has been examined from the following localities: KANSAS: Clarke Co., May, 1962 ft. (F. H. Snow); MANITOBA: Onah, VI–21 '21 (N. Criddle, P. Vroom); MINNESOTA: Anoka, VI–23 '36 (H. R. Dodge), St. Paul, VI–27 '35 (A. B. Gurney); MONTANA: Glendive, VI–17 and 18 '30 (C. N. Ainslie); NEBRASKA: Neligh, VI–19 '09 (J. T. Zimmer); WYOMING: '81 (Morrison).

The fact that the type is a female rather than a male explains the name "flavipes," as the females have the basal two-thirds, five-sixths, and thirteen-sixteenths, respectively, of the fore, middle, and hind femora yellow. In the males only the basal one-tenth, one-half and five-eighths of the femora are yellow. The scutellum is densely gray-pollinose with the narrow posteriormargin shining black, hairs white, those on the disc appressed, and with about 10 erect marginals. The pulvilli are subequal to the claws in length.

Laphystia howlandi, new species

Male: Length 8 mm. Head densely white-pollinose, palpi and proboscis black. Hairs and bristles white, mystax composed entirely of hairs about as long as the first two antennal joints. Face at antennae subequal to width of one eye. Antennae black, first joint 1½ times as long as second, first with 3 to 4 strong white bristles below, sparse hairs of both white; third subequal in length to first two; style narrow, one-third as long as third.

Mesonotum densely white-pollinose, with a golden cast over the large central area imparted by the short hairs; sparse, golden-white, erect hairs over entire notum but more numerous anteriorly. Bristles white, two or three presutural, two or three supraalar, and two or three postalar; three or four longer golden hairs posteriorly in the dorsocentral rows. Pleurae and coxae densely white-pollinose and -haired, mesopleurae with a golden tinge. Scutellum densely golden-pollinose, the narrow posterior margin black at middle, sparse long, erect, white hairs over entire notum, shorter hairs golden.

Abdomen reddish-brown, first segment largely and a central spot on segments 3 to 6 darker brown. Hairs white, short, appressed, but longer on sides of segments 1 and 2; one to five short, white bristles on the sides of the segments. Pollen gray on first segment, golden on others; segments 1 and 2 wholly pollinose except for a narrow bare spot on each side basally, segment 3 largely pollinose but with larger bare spots on each side basally, segments 4 to 6 with complete

posterior fasciae, segment 4 with a suggestion of pollen at middle, more or less dividing the bare area. Genitalia light to dark brown, hairs white. Venter gray-pollinose; sparse, erect hairs white.

Femora yellowish, the apical one-fourth of the fore and middle pairs and the hind ones wholly brownish-black dorsally, all gray-pollinose above; basal two-thirds of fore and middle, and basal one-half of hind tibiae yellowish, apically brown; tarsi brown; claws black, brownish on basal one-third; pulvilli white, three-fifths the length of the claws; empodia brown. Hairs and bristles white to yellowish.

Halteres yellowish, lower stem brown; alulae yellowish. Wings hyaline, veins brown; anterior crossvein slightly before middle of discal cell.

Female: Length 9 mm. Similar to male. Abdominal segments 7 and 8 wholly yellowish-gray-pollinose; terminalia brown, hairs white. Mesonotum without sparse erect hairs except anteriorly. Anterior crossvein at two-fifths length of discal cell.

Holotype: Male, Indio, Calif., V–13 '48 (J. Wilcox). *Allotype:* Female, same data (A. F. Howland). *Paratypes:* 62 males and 45 females, same data, V–25 '48, and 9 miles south of Indio, Calif., IV–1, V–12, 13, and 19 '48 (Howland and Wilcox). Three males and three females, Laguna Lake, Imperial Co., Calif., VI–9 to 11'50, University of California (Los Angeles). Four males and eight females, 12 mi. E. Heber, Imperial Co., Calif., V–11 to 23 '56 (T. R. Haig), University of California (Davis).

Sparse, erect hairs on the notum of the scutellum are found only in this species and in *utahensis*, new species. In the *opaca* group the erect hairs on the scutellum are dense.

Laphystia jamesi, new species

Male: Length 11 mm. Head black, densely white-pollinose; palpi and proboscis shining. Mystax white, dense, hairs as long as first two antennal joint and extending to antennae; hairs otherwise white, numerous on frons and ocellar tubercle; occipital bristles white. Face at antennae subequal to width of one eye. Antennae brownish-black, first joint wider and 1⅓ times as long as second, with two or three whitish bristles below, both white-haired; third slightly longer than first two together; style narrow, three-eighths as long as third.

Mesonotum black, gray-pollinose, the central stripe blackish, before suture narrowly bisected, behind bare of pollen; intermediate area behind suture, and narrowly before suture mesally, bare of pollen. Hairs white, rather dense, semierect, and as long as first antennal joint, longer on the margins. Bristles white, three presutural, three supraalar and three postalar. Pleurae and coxae densely white-pollinose with a slight golden tinge, hairs white. Scutellum shining black, white-pollinose laterally and posteriorly so that the middle half of the posterior margin and three-fourths of the disc are shining and confluent at the middle one-fourth; hairs white, sparse, semierect on disc, about 25 long, erect hairs on posterior margin.

Abdomen black, sides and posterior margins gray-pollinose, the fasciae separated at middle by about one-fourth the width of the segments, that on segment 6 entire. Hairs short, appressed, white (on black areas yellowish), longer on sides of first two segments; bristles white, varying from three to six per side of the segments. Genitalia brown, hairs yellowish-white. Venter entirely gray-pollinose; long, sparse, erect hairs white.

Trochanters black; femora black, the knees and hind ones narrowly at base, reddish; densely white-pollinose except venter of hind pair. Tibiae black apically, about the basal one-half yellowish; tarsi black; claws black, basal half yellowish; pulvilli whitish, as long as claws; empodia brown. Hairs and bristles white.

Halteres yellowish-white, base brown. Wings light brown, veins brown; anterior crossvein slightly before middle of discal cell; petiole of anal cell half as long as anterior crossvein.

Female: Length 12 mm. Similar to male. Pollen all over more golden. Abdominal bristles more numerous, varying from 7 to 15 per side of segments.

Holotype: Male, Long Beach, Calif., V–8 '57 (J. Wilcox), in the James collection. *Allotype:* Female, same data, V–6 '57, in the James collection. *Paratypes:* 38 males and 25 females, same locality, V–6 to 13 '57 (G. T. Karamanos, A. F. Howland, Wilcox). One male and two females, Long Beach, Calif., VI–25 '35 (M. T. James), in the James collection. One male, San Diego Co., Calif. (Coquillett Coll.), in the U. S. N. M. One female, San Diego, Calif., IV–26 '91 (F. E. Blaisdell), and male and female, San Diego, Calif., V–13 and 19 '15 (E. P. Van Duzee), in the California Academy of Sciences.

More than 15 years ago, Dr. James gave me the street address where his specimens were collected, in a vacant lot about 4 miles from the ocean. Repeated attempts revealed no additional specimens in this area. They were finally found on the saline flats near the San Gabriel River and about ½ mile from the ocean.

Laphystia laguna, new species

Male: Length 9 mm. Head black, densely white-pollinose, palpi and proboscis shining. Hairs white, mystax long, extending to antennae, occipital bristles white. Face 1⅕ times as wide as one eye. Antennae brown, first joint broader and 1⅓ times as long as second, white-haired, the first with three white bristles below, third joint subequal to length of the first two, style slender and nearly one-half as long as third joint.

Mesonotum brownish black, gray-pollinose, the bisected central stripe and intermediate area light

brown, with a narrow bare spot before and behind the suture just outside the dorsocentral rows. Erect hairs marginally, and scattered ones before the suture, white, about as long as first antennal joint, the short, appressed hairs on dorsum golden brown. Bristles yellowish-white, two or three presutural, three or four supraalar, and two postalar. Pleurae and coxae densely gray-pollinose and white-haired. Scutellum densely grayish-golden-pollinose, the narrow posterior margin bare, erect marginal and discal hairs white.

Abdomen dark brown, the anterior and posterior margins narrowly light brown. Short, appressed hairs on pollinose areas, and longer hairs on the sides of the first three segments, white; appressed hairs on bare areas golden-brown. Sides and posterior margins white-pollinose with a golden cast, first segment almost wholly, posterior one-half of 2 to 4, posterior one-third of 5, and the posterior one-fourth of 6, pollinose; fasciae narrowly interrupted at the middle on segment 4 and by about one-fifth the width of abdomen on 5. Genitalia brown, with white and yellowish hairs. Venter yellowish-gray-pollinose and with white hairs.

Legs brownish black; basal one-sixth of fore, one-third of middle, and five-ninths of hind femora, and knees of all narrowly, yellowish; basal one-half of fore and middle and two-thirds of hind tibiae, yellowish. Hairs and bristles white, femora white-pollinose apically; claws brown, the apical one-fourth reddish, pulvilli white, seven-eights as long as claws, empodia light brown.

Halteres light brown basally, stem and knob yellow. Alulae yellowish white, short hairs white. Wings hyaline, veins brown; anterior crossvein at five-twelfths length of discal cell.

Female: Length 10 mm. Similar to male. Pollen of face and front with a golden tinge. Mystax not as long, but extending to antennae. Pollinose fasciae on segments 4 and 6 of abdomen narrowly interrupted, segment 5 as in male, narrow segments 7 and 8 wholly pollinose, terminalia brown with white hairs. Basal one-third of fore, one-half of middle, and seven-ninths of hind femora, yellowish-red. Pulvilli four-fifths as long as claws.

Holotype: male, Laguna Madre, 25 mi. S.W. of Harlingen, Texas, IV–10 '45 (D. E. Hardy, V. L. Wooley), in the U. S. National Museum. *Allotype:* female, same data, in the U.S.N.M. *Paratypes:* two males and three females, same data.

Most nearly related to *litoralis* Curran, which so far has only been taken along the Atlantic coast but not on the Gulf of Mexico. Besides the darker legs, *litoralis* has the mesonotum wholly pollinose, with long, erect hairs behind as well as before the suture, the erect scutellar hairs are more numerous, and there are long hairs on the sides of all the abdominal segments.

Laphystia lanhami James

Laphystia lanhami James 1941, Jour. Kansas Ent. Soc. 14: 35–36.

Types (both sexes) Delta, Colo., June 25 to July 8, 1938 (R. Bauer and U. Lanham) in the Colorado A. and M. College collection.

A pair of paratypes have been available for study, and other specimens have been seen from the following localities. COLORADO, north of Uravan, VII–15 '41 (B. Rotger, C.R.). NEW MEXICO, near Grants, VII–4 '40 (B. Rotger C.R.).

These specimens have the first abdominal segment largely pollinose, the second with anterior and posterior fasciae, the third with a posterior fasciae narrowly interrupted at the middle, the fourth and fifth without posterior fasciae but with the sides pollinose, and the sixth with the fasciae entire. James (1941) has indicated that the fasciae, especially of the males, are variable but that the one on the second segment (first segment in this paper) is always entire. Pulvilli are six-sevenths as long as claws.

See note under ***rubra***.

Laphystia limatula Coquillett

Laphystia limatula Coquillett 1904, Proc. Ent. Soc. Washington 6: 180.
Laphystia limatula, Hermann 1908, Berlin Ent. Zeitschr 43: 152.
Laphystia limatula, Back 1909, Trans. Amer. Ent. Soc. 35: 229.
Laphystia limatula, Curran 1927, Canadian Ent. 49: 86.
Laphystia limatula, Curran 1931, Amer. Mus. Novitates No. 487: 12.

This species was described, apparently from a single male specimen, from La Luz, New Mexico (C. H. T. Townsend), type No. 7951 U.S.N.M. A pair from a series collected at Tempe, Arizona, July (D. K. Duncan), were compared with the type by Mr. C. T. Greene, who said: "In these notes I am giving only the differences. Otherwise the types and your specimens are identical. Long white hairs on the front like in the type. Specimen marked 'X'—white hairs on the front like in the type. Scutellum—bristles white; apical pair and a single one near each basal angle small and hair-like; a row of four large white bristles on each side of apex. Thorax—dorso-central portion more golden." The specimen marked 'X' was the male.

Female: Length 10 mm. Head white-pollinose, face and frons with a yellowish tinge. Hairs and bristles white, mystax with about 16 oral bristles, hairs above short. Antennae brown, hairs white, first joint with two strong bristles below.

Mesonotum yellowish-gray-pollinose; short, appressed hairs white. Bristles white, two presutural, two or three supraalar, and two or three postalar. Pleura gray-pollinose, hairs white. Scutellum yellowish-gray-pollinose, short, appressed, discal hairs white; five white marginal bristles and several longer white hairs.

Abdomen yellowish brown, basal two segments slightly darker; short, appressed hairs black on bare areas, white on pollinose areas, slightly longer on sides of first segment; lateral bristles white. Posterior fasciae white-pollinose, entire on segments 1 to 3, with a slight basal emargination on 2 and 3 and a deep basal V-shaped emargination on 1, narrowly interrupted on 4, interrupted by about one-fourth the width of the segments on 5 and 6. Segments 7 and 8 narrow, wholly pollinose; genitalia brown, hairs white.

Coxae and trochanters yellowish, coxae densely white-pollinose and white-haired. Femora yellow, apical one-third of fore and middle, and apical two-fifths of hind pair dorsally, brownish black. Basal one-third of tibiae yellowish, remainder and tarsi brownish black; hairs and bristles white; claws black, basal one-third yellowish; empodia brown; pulvilli white, four-fifths as long as claws.

Halteres and alulae yellowish white, fringe white. Wings yellowish hyaline, veins yellowish to brown; anterior crossvein at one-third length of discal cell.

Hypotype: female, Tempe, Ariz., July (D. K. Duncan) deposited in the U.S.N.M.

Other specimens seen are from the following localities. ARIZONA: Tempe, July (D. K. Duncan), both sexes; Cochise, VIII–21 '35 (E. I. Beamer). NEW MEXICO: Alamogordo, VII–14 '38 (M. B. Jackson).

Laphystia litoralis Curran

Laphystia sexfasciata, Back 1909, Trans. Amer. Ent. Soc. 35: 228–229 (misidentification, not Say).
Laphystia litoralis Curran 1931, Amer. Mus. Novitates No. 487: 16–17.

Described from 4 males and 10 females (including types) from Rockaway, N. Y., VIII–13 and 19 '03 (J. L. Zabrisky), and one female, Avalon, N. J., VII–29 '14, in the American Museum of Natural History.

Back gave the following localities: Avalon, N. J., VII–29, VIII–2, 15, 27; N. Y., VIII–10; N. C.; Fla., Capron, IV–19, and St. Augustine (Common along seashore, June, July, C. W. Johnson); Ga.; Tex.

Specimens have been examined from the following localities. FLORIDA: Daytona, IV–6 '20 (P. W. Fattig); Daytona Beach, X–21 '38 (G. P. Engelhardt); Duval Co., VIII–31 '55 (H. V. Weems, Jr.); Farmdale, VI–27 '48 (R. H. Beamer). GEORGIA: Savannah, X–3 '28 (Brooklyn Mus. Coll. 1929); St. Simons Island, VIII–31 '30 (Fattig). NEW JERSEY: Avalon, VII–29 '94 (J. M. Aldrich Coll.) NEW YORK: Rockaway (paratypes). NORTH CAROLINA: Carolina Beach, X–6 '34 (F. S. Blanton). VIRGINIA: Cape Henry, VIII–31 '16 (R. C. Shannon); Virginia Beach, IX–13 '13 (Fred K. Knab).

Laphystia martini, new species

Male: Length 8 mm. Head black, densely white-pollinose; cheeks, palpi and proboscis shining. Occipital and oral bristles and hairs white; mystax dense but extending only half-way to antennae; short, erect hairs on frons and ocellar tubercle rather numerous; face at antennae subequal in width to one eye. First antennal joint and style brown; remainder yellowish red; hairs white; two white bristles below on first joint; first and second joints subequal in length, the third about four-fifths as long as first two together; style one-fourth as long as third.

Mesonotum black, densely gray-pollinose, the central stripe and intermediate area obscurely brown; the dorsocentral stripe for a short distance before and behind the suture, and short, narrow, lateral spots and a central spot before the scutellum, bare of pollen. Hairs short, appressed, yellowish, a few longer white ones on and behind humeri. Bristles white, two or three presutural, one or two supraalar, and two postalar. Pleura and coxae densely gray-pollinose, with a slight golden tinge, hairs white, rather long on mesopleura. Scutellum densely gray-pollinose, the central two-thirds of posterior margin, and venter, bare of pollen; sparse, recumbent discal hairs yellowish, posterior margin with about 20 very short, brownish hairs. Postscutellum densely gray-pollinose, narrowly shining black at the middle.

First and sixth abdominal segments brown, the remainder yellowish-brown, wholly gray-pollinose except the narrow anterior and posterior margins and the central, basal one-fifth of the sixth segment. Coarse recumbent hairs yellowish dorsally and white laterally, bristles white. Genitalia brown and reddish-brown, white-haired. Venter densely gray-pollinose, short, recumbent, white-haired.

Legs including trochanters reddish-brown; dorsum of femora, tarsi, and apical three-fourths of tibiae brown, color of femora and tibiae largely obscured by dense gray pollen. Hairs and bristles white; claws black, basal one-fifth reddish; pulvilli white, one-fourth as long as claws; empodia light brown.

Halteres reddish-white, lower stem brown; alulae brownish, margin and fringe white. Wings hyaline, veins dark brown; anterior crossvein at three-sevenths length of discal cell; first posterior cell closed and petiolate, the petiole slightly longer than length of anterior crossvein.

Female: Length 10 mm. Similar to male. Face and frons golden-pollinose; mystax extending about one-third the distance to antennae; hairs on frons and ocellar tubercle shorter; first antennal joint with one strong bristle below. Abdomen wholly brownish, segments 3 and 4 with small lateral-anterior spots bare of pollen, segment 5 with large spots, segment 6 with basal two-fifths (except laterally) bare of pollen; segments 7 and 8 wholly pollinose, apical bristles white; ovipositor brown, hairs yellowish-white.

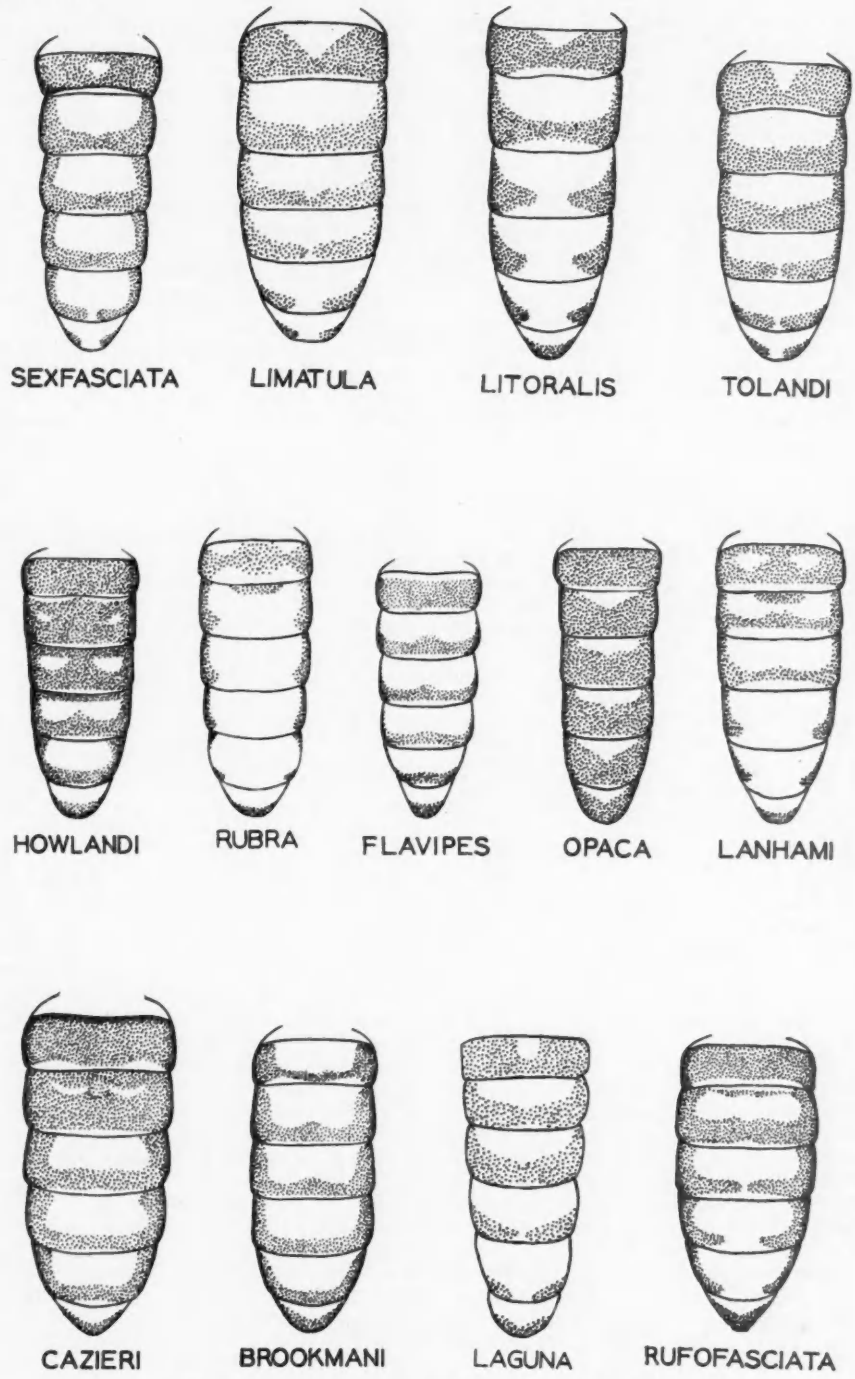

FIG. 2.—Pollinose patterns of the abdomen of *Laphystia* species. Males are illustrated, except for *L. confusa* and *L. texensis* All are drawn to the same scale. Pollinose areas are indicated by stippling.

Holotype: male, Temecula, Calif., VI–30 '56 (J. Wilcox). *Allotype:* female, same data. *Paratypes:* 116 males and females, VI–30 to VII–21 '56 (C.H. and Dorothy Martin, Guy F. Toland, Itol J. and J. Wilcox). One female, Calipatria, Calif. (Imperial Co.), V–26 '56 (T. R. Haig). Four males, three females, Borrego Vly., Calif. (San Diego Co.), dunes, IV–18 '57 (R. C. Bechtel, J. C. Hall), University of California (Davis).

The closed first posterior cell, almost wholly pollinose abdomen, mystax confined to the lower half of the face, very short pulvilli, and postscutellum bare of pollen at the middle, are all characters not found in the other species.

A few specimens have a narrow anterior indentation at the middle of the abdominal segments bare of pollen, and one specimen of each sex has the anterior one-fourth of segments 2 to 6 bare of pollen except laterally.

Laphystia notata (Bigot)

Triclis notata Bigot 1878, Ann. Soc. Ent. France (5) 8: 433. Type locality: Texas.

Laphystia sexfasciata Say, Bigot 1879, Ann. Soc. Ent. France (5) 9, Bull. p. lxviii (with *T. notata* as synonym). "*Laphystia subfasciata* Osten Sacken,"[5] Bigot 1879, Ann. Soc. Ent. France (5) 9: 236.

Laphystia notata, Williston 1885, Trans. Amer. Ent. Soc. 12: 85.

Laphystia notata, Curran 1931, Amer. Mus. Novitates No. 487: 10–14.

Bigot (1879) made his *Triclis notata* a synonym *Laphystia sexfasciata* Say, and, according to Curran (1931), removed the labels from his specimens so that they cannot now be identified in the Hope Museum at Oxford. Curran (1931) considered *notata* a valid species, and gave a description of both sexes from Galveston, Texas, and of a female from Lawrence, Kansas.

Specimens have been examined from the following localities. MISSISSIPPI: Rosedale, VI–25 '22. TEXAS: Galveston, VI–10 '17 (J. M. Aldrich), VI–16 '00 (Collection Aldrich), May (F. H. Snow), Jn. '00 (W. M. Wheeler collection) A.M.N.H. Dept. Invert. Zool. No. 6088; Matagorda, V–5 '53 (R. H. and L. D. Beamer); 10 mi. N. Rockport, IV–18 '52 (Michener, Wille, Beamer, La Berge), taken on *Gaillardia*.

The abdominal fasciae are separated by about one-half the width of the segments in the males, and by a little less than one-half in the females; the basal half of the hind femora is reddish, as is the basal half of the claws; in males the broad, central, black stripe of the mesonotum is confluent with the intermediate area, in females wholly pollinose; the mesonotal hairs before the suture are about as long as the first antennal joint, sparse in females.

The *notata* group has the scutellum wholly pollinose, with recumbent discal hairs and longer, erect, marginal hairs. The pollinose fasciae are interrupted on abdominal segments 1 to 5, entire on 6. This group occurs from New Mexico to Florida, and from Texas to Manitoba. The species have been separated mainly on the color of the legs and the pollinosity and pilosity of the thorax and abdomen, characters which, with the limited material available, seem variable. With more material a more satisfactory arrangement should be possible.

Laphystia ochreifrons Curran

Laphystia ochreifrons Curran 1931, Amer. Mus. Novitates No. 487: 16.

Holotype, female, Kentucky, July 16, and one paratype female, Ohio, in the American Museum of Natural History.

Male: Length 9 mm. Head densely white-pollinose with a slight yellowish tinge on the frons; mystax and hairs white; occipital and bristles on the first antennal joint pale yellowish. Face subequal in width to one eye.

Margins of mesonotum, including humeri, gray-pollinose with a yellowish tinge; the broad central stripe and confluent intermediate area black, the central stripe bisected anteriorly. Hairs yellowish-white, appressed on the dorsum but mostly about as long as the first antennal joint. Scutellum entirely yellowish-gray-pollinose, the disc with short, recumbent, yellowish hairs and the posterior margin with about 20 fine, erect, white hairs.

Abdomen black, pollinose fasciae on segments 2 to 5 separated by about four-sevenths the width of the segments as viewed from above, separation wider on first segment, fascia on segment 6 entire.

Femora black, the knees and basal one-sixth of the hind ones reddish; about the basal one-third of tibiae reddish, remainder and tarsi, black. Pulvilli subequal to claws in length.

Wings light brown, veins light brown; anterior crossvein at two-fifths length of discal cell.

Hypotype: Male, labeled "Ky. 7/15/'1" in the writer's collection.

This and another male labeled "Ky. 7/16/'1" were sent to me in 1929 by the late Professor James S. Hine, labeled *L. sexfasciata* Say. There is a male in the Pritchard collection, also a female in the U.S. National Museum, with the same label. The fasciae on the female abdomen are separated by five-sixths the width of the segments.

These are the only specimens seen which are typical of *ochreifrons*. Others placed here tentatively are as follows. FLORIDA: Liberty Co., Rock Bluff Landing, VI–1 '24 (T. H. Hubbell No. 228). GEORGIA: Cairo, VI–19 '31 (P. W. Fattig); Macon, V–14 '32 (Fattig); Ochlochnee, V–27 '39 (Fattig); and Thomasville, VI–30 '48 (E. L. Todd). LOUISIANA: Baton Rouge, V–24 '32 (T. H. Roberts), and V–28 and 29 '37 (Fred Snyder). MISSISSIPPI: Rosedale, VI–21 '22.

[5]This was a lapsus calami on Bigot's part, as Osten Sacken (1878) Cat. Dipt., ed. 2, wrote *sexfasciata*.

In most specimens the first posterior cell is narrowed, and in some is closed at the margin of the wings. Specimens from Georgia have the abdominal fasciae separated by four-sevenths the width of the segments in the males, but by less than one-half the width of the segments in the females; the recumbent hairs on the dorsum are brown or black on the nonpollinose areas, and on segments 4 and 5 they reach the lateral margins anteriorly. The specimens from Louisiana are smaller, and have the fasciae separated by a little less than one-half the width of the segments.

Laphystia opaca Coquillett

Laphystia opaca Coquillett 1904, Proc. Ent. Soc. Washington 6: 180.
Laphystia opaca, Back 1909, Trans. Amer. Ent. Soc. 35: 229–30.
Laphystia opaca, Curran 1931, Amer. Mus. Novitates No. 487: 14.

According to Back, the single male type (Cat. No. 7952, U.S.N.M.) is from Padre Island, Tex., June 29 (C. H. T. Townsend). Back mentioned two males and one female from Galveston, Texas, June 5 (W. M. Wheeler) in the American Museum of Natural History, apparently part of the series described as *texensis* by Curran.

Only three male specimens have been seen which can be assigned to this species. Texas, Beach 17 mi. W. Sabine Pass, VI–10 to 12 '56 (H. E. Evans, E. G. Matthews), and Cameron Co., 8–3 '28 (R. H. Beamer); and Louisiana, Cameron, VI–17 '48 (R. H. Beamer).

See note under *Laphystia texensis* Curran, below.

Laphystia rubra Hull

Laphystia rubra Hull 1958, Psyche 64(2): 74–75.

Type, female, near Navajo, Ariz., VII–11 '54 (F. M. Hull), in the Hull collection. The male is described below.

Male: Length 8 mm. Densely white-pollinose, palpi and proboscis black. Hairs and bristles white, bristles on oral margin about twice as long as the hairs above, face at antennae five-sixths as wide as one eye. Antennae black, first joint 1¼ times as long as second, both sparsely short-white-haired, the first with three yellowish bristles below; third subequal in length to first two, style two-fifths as long as third.

Mesonotum gray-pollinose, the divided central stripe and intermediate area appearing darker; over all with a golden tinge due to very short appressed hairs. Bristles yellowish, two presutural, two supraalar and two postalar. Pleurae gray-pollinose and white-haired. Scutellum gray-pollinose, the narrow posterior margin at middle black, over all with golden tinge due to short, appressed hairs.

Abdomen reddish-brown, hairs short, golden, appressed, bristles yellowish-white with from two to five on the sides of each segment. Pollen grayish-golden, dense on sides of all segments, posterior fasciae entire on segments 1, 2, and 6, narrow and interrupted at middle on 3, very broadly interrupted on 4 and 5; on segment 2 a narrow anterior fasciae does not reach lateral margins. Genitalia brown, hairs white. Venter gray-pollinose, sparse appressed hairs white.

Trochanters brownish-black; femora yellowish, gray-pollinose, dorsal four-fifths of fore, one-half of middle, and entire hind pair, brown apically; basal one-half of tibiae yellowish, apex and tarsi brown; claws black, basal one-third yellowish; empodia brown; pulvilli whitish, subequal in length to claws. Hairs and bristles white.

Halteres yellowish, base brown; alulae yellowish white. Wings pale brown, veins brown, anterior crossvein at one-third length of the discal cell, anal cell short petiolate.

Hypotype: Male, Beaver Dam Wash, U. S. Highway 260, Ariz., VI–30 '49 (C. H. Martin) in the Martin collection.

Other specimens, same locality, VI–30, VII–1, and VIII–1 '49 (C. H. and Dorothy Martin, Itol J. and J. Wilcox). COLORADO: Allison, 6200', VII–30 '41; Arboles, 6000', VII–4 '38; Dolores Riv., VII–15 '41; La Posta, 6000', VI–22 '36; and north of Uravan, VII–15 '41 (B. Rotger, C.R.).

Normal specimens have the pollinose fasciae entire on abdominal segments 1 and 2, but in others these fasciae are faded, indistinct, or lacking. This species is very close to *lanhami* James and might prove to be a reddish variation thereof.

Laphystia rufiventris Curran

Laphystia rufiventris Curran 1931, Amer. Mus. Nov. No. 487: 17–18.
Laphystia rufiventris, James 1941, Jour. Kansas Ent. Soc. 14: 35.

Described by Curran from a single female collected at Green River, Wyo., VII–2 '20 (F. E. Lutz), in the American Museum of Natural History. James partially described a female taken 5 miles north of Delta, Colo., VI–30 '38 (R. Bauer). The male is described below.

Male: Length 10 mm. Head densely white-pollinose, hairs and bristles white, oral bristles most numerous at center. Face subequal in width to one eye. Antennae with first joint black, remainder brown, first broader and subequal in length to second, both white-haired, the first with two or three whitish bristles below; third slightly longer than the first two, style about one-fourth as long as third.

Mesonotum gray-pollinose, central stripe and intermediate area appearing black at some angles; hairs very short, white, appressed, scattered longer ones on margins. Bristles whitish, two or three presutural, two supraalar, and one or two postalar. Pleurae and coxae densely gray-pollinose and white-haired. Scutellum gray-pollinose, narrow central half of posterior margin black, hairs appressed, white, one long marginal

hair near middle and two or three shorter ones at sides.

First abdominal segment, basal four-fifths of second, and sides of segments 3 to 6 (decreasing in extent apically) brownish black; segments 4 to 6 yellowish-red, 3 and apex of 2 slightly darker. Narrow sides and posterior margins gray-pollinose, interrupted by five-eights the width of abdomen on segments 1 and 4, by one-half on 2 and 3, and much more widely on 5 and 6. Short, appressed hairs white, bristles yellowish. Genitalia brown, hairs white. Venter brown, becoming lighter on segments 5 and 6, sparsely white-haired, gray-pollinose, segments 3 to 6 with bare areas at middle.

Legs black, narrow base and apex of femora reddish, and about the basal one-sixth of tibiae yellowish; hairs white, bristles white to yellowish; claws black, reddish basally; pulvilli white, three-fourths length of claws; empodia brown.

Halteres yellow, base brown; alulae yellowish, broad margin and hairs white. Wings hyaline, veins brown; anterior crossvein at two-fifths length of discal cell.

Hypotype: male, Green River, Wyo., VI–21 '50 (C. H. Martin), in the Martin collection.

One other male, Grand Junction, Colo., V–24 '26 (M. C. Van Duzee collection).

This is the only species which has the pollinose fascia broadly interrupted on abdominal segment 6. In the *sexfasciata* group there is or tends to be a narrow interruption on this segment.

Laphystia rufofasciata Curran

Laphystia rufofasciata Curran 1931, Amer. Mus. Nov. No. 487: 13.

Holotype, male, Green River, Wyo., VII–2 '20; allotype, female, Rock Springs, Wyo., VI–19 '20 (F. E. Lutz), in the American Museum of Natural History.

Specimens are at hand from the following localities. COLORADO: Rangely, 5300', VII–15 '41 (B. Rotger, C.R.). WYOMING: Green River, VII–2 '20 (F. E. Lutz) and VI–20 '50 (C. H. Martin); Rock Springs, VI–9 '58 (J. Wilcox).

With a fair series of specimens at hand, certain variations are evident. Normal specimens have the first abdominal segment largely, and segments 2 to 6 with the sides and posterior margins, yellowish-gray-pollinose; the fasciae are narrowly interrupted on 3, and interrupted by about one-fourth the width of the abdomen on 4 and 5. Some specimens have segment 2 largely pollinose, and the fasciae entire on the remainder; while in others the fasciae on segments 4 and 5 are broadly interrupted. The legs vary from having the dorsum of the fore and hind femora almost wholly, and the apical two-thirds of the dorsum of the middle femora, black; to specimens with the apical one-third of the fore and just the tips of the middle and hind femora, black. The pulvilli are subequal to the claws in length.

Laphystia sexfasciata (Say)

Dasypogon 6-fasciatus Say 1823, Jour. Acad. Nat. Sci. Philadelphia 3: 50; Complete Works 2: 64.

The original description was as follows:

"1. D. 6-FASCIATUS.—Cinereous; abdomen black, with white bands on each segment.

"Inhabits Missouri.

"Body black, densely covered with short cinereous hair; head with longer silvery hair; antennae black; nervures fuscous; tergum black; polished, each segment with a white band at tip, a little dilated in the middle, and occupying about one-third of its proper segment; thighs and tibia testaceous at base; halteres pale.

"Length seven-twentieths of an inch."

Say's type being lost, identification of *sexfasciata* is a problem. Curran (1927) identified specimens from Manitoba as this species, and considered *flavipes* Coquillett a synonym. This solution is possible; but it seems more logical to select specimens from Say's "Missouri," which included all or parts of the present states of Missouri, Iowa, Kansas, Nebraska, and Colorado. Weiss and Zeigler (1931), in their account of Say's first western expedition, related that the summer of 1819 was spent traveling west along the Missouri River, with short trips into the adjacent territory, the winter (September 26, 1819, to June 9, 1820) was spent 5 miles south of Council Buffs on the west bank of the Missouri River, and the remainder of 1820 was spent traveling along the Platte River to Denver and back through Kansas via the Arkansas River.

Male: Length 10 mm. Head black, densely white-pollinose except palpi and proboscis. Hairs and bristles white, mystax about as long as first two antennal joints and reaching antennae; occipital bristles yellowish. Antennae black to brownish; first two joints white-haired, the first with three whitish bristles below; third slender and subequal in length to first two; style one-fourth as long as third.

Mesonotum brownish-pollinose; narrow central stripe, intermediate area, lateral margins, transverse suture, and humeri gray-pollinose. Hairs dorsally short, appressed, golden; anteriorly, on humeri, laterally and posteriorly, white, erect, and about as long as first antennal joint. Bristles yellowish, three presutural, four supraalar and three or four postalar. Pleura and coxae densely white-pollinose, with a slight golden tinge, hairs white. Scutellum gray-pollinose, the posterior margin shining black; discal hairs short, appressed, golden; four yellowish marginal scutellar bristles and a few long marginal hairs.

Abdomen black; first segment largely and the posterior one-third of segments 2 to 6 gray-pollinose, the fasciae very narrowly interrupted on 4, on 5 by one-sixth, and on 6 by about one-third the width of the respective segments. Hairs white, longer on sides of first segment, short,

white, appressed on fasciae, and short, appressed, golden on black areas. Lateral bristles white, varying from four to seven per side per segment. Genitalia black, hairs white.

Legs, including trochanters, brownish-black; about the basal one-third of fore and basal one-half of middle and hind femora, basal one-half of fore and hind tibiae and basal three-fourths of middle tibiae, yellowish-red. Claws black, the basal one-third reddish; pulvilli white, seven-eighths as long as claws; empodia brown.

Halteres yellowish, lower stem brown. Wings light brown, veins light brown; anterior crossvein at two-fifths length of discal cell.

Neotype: Male, Lincoln, Nebr., VI–25 '36 (R. W. Dawson), in the Pritchard collection. *Neoallotype:* Female, same data, in the Pritchard collection.

Other specimens seen are as follows. KANSAS: Clark Co., 1962 ft., May and June (F. H. Snow). NEBRASKA: Lincoln, VI–21 '12 (R. W. Dawson, L. M. Gates), VI–25 '36 (Dawson), and VII–3 '09 (C. H. Gable).

Laphystia snowi new species

Male: Length 8 mm. Head white-pollinose, palpi and proboscis black; the dense hairs and bristles white. Antennae black, first joint broader and 1⅓ times as long as second, both white-haired, first with about six short white bristles below; third joint of about uniform width and 1⅓ times as long as the first two joints together; style one-fourth as long as third joint.

Mesonotum whitish-pollinose, the broad lateral spots appearing black at some angles. Hairs white, rather long, erect on the anterior half and posteriorly, those behind the suture on the sides appressed, yellowish. Bristles yellowish, two presutural, two supraalar, and two postalar. Pleura and coxae densely whitish-pollinose and white-haired. Scutellum densely whitish-pollinose, the narrow margin black, hairs white, longer and erect on posterior margin.

Abdomen shining black, segments 1 to 6 laterally whitish-pollinose, as are the narrow posterior fasciae which are narrowly interrupted on segments 4 and 5 and entire on the others. Hairs white, longer on the sides of first segment; short, appressed, and yellowish dorsally; bristles white, about four on sides of first two segments, and two each on remaining segments. Venter entirely pollinose and white-haired. Genitalia shining brown and white-haired.

Femora yellowish, about the apical one-half of fore ones and the apical one-fourth of middle and hind ones, above, blackish; tibiae yellowish, the apical one-fourth of fore and middle ones and nearly the apical one-half of hind ones, blackish; tarsi blackish; claws black, bases reddish; pulvilli light brownish, subequal to claws in length; hairs and bristles white.

Halteres yellowish, the narrow base brown. Wings hyaline, veins light brown; anterior crossvein at about two-fifths length of discal cell.

Female: Length 8 mm. Similar to male. Pollen of head and mesonotum with a yellowish tinge, hairs of mesonotum largely appressed. Femora and tibiae yellowish, tips of fore femora and tips of tibiae blackish. Only the fasciae on abdominal segment 5 interrupted.

Holotype: Male, Clark Co., Kans., June, 1962 feet (F. H. Snow), in the Snow Collection, University of Kansas. *Allotype:* Female, same data, May, in the Snow Collection. *Paratypes:* 16 specimens, same data.

Most of the specimens of both sexes have the legs as described for the male; the pollinose fasciae on abdominal segments 3 to 5 of some of the males are interrupted. Very close to and possibly only a variant of *flavipes* Coquillett. The more extensive yellow color of the legs, and the narrow sides and posterior fasciae interrupted on segments 3 to 5 or 4 and 5, are constant in the material available.

Laphystia sonora, new species

Male: Length 11 mm. Head black; cheeks, palpi, and proboscis shining; remainder densely white-pollinose. Hairs white, lower half of mystax long, upper half with hairs about as long as first antennal joint; occipital bristles yellowish. Face at antennae slightly wider than width of one eye, in profile more gibbous than most species. First antennal joint broader than and 1½ times as long as second, both white-haired, the first with a whitish bristle below; third equal to length of first two together, style one-fourth length of the third.

Mesonotum yellowish-gray-pollinose, the central stripe and intermediate areas subshining, black. Hairs white, mostly erect and about as long as second antennal joint, longer anteriorally and posteriorly. Bristles yellowish, two presutural, three supraalar and three postalar. Pleura and coxae densely gray-pollinose and white-haired. Disc of scutellum subshining, black, posterior margin densely gray-pollinose; hairs white, short, erect, with about 12 longer ones on posterior margin.

Abdomen black, hairs white, those dorsally semierect and yellowish, bristles yellowish-white. Sides and posterior margins densely gray-pollinose, the fasciae interrupted at middle by about two-sevenths the width of the abdomen on segments 1 to 5, entire on 6. Genitalia black, with short, white hairs. Venter grayish-yellow-pollinose and long, erect, white-haired.

Legs black, narrow tips of the femora and basal one-sixth of hind femora, basal one-third of fore and middle tibiae and basal one-half of hind tibiae, reddish-brown. Fore and middle femora largely gray-pollinose. Hairs white, bristles yellowish-white; basal one-thrd of claws reddish,

apically black; pulvilli white, almost as long as claws: empodia brownish

Halteres whitish with brownish mottling, base brown; alulae light brownish, margin and fringe white. Wings light brownish, tending to be hyaline basally; veins brown; anterior crossvein at two-fifths length of discal cell, first posterior cell open, petiole of fourth posterior cell twice as long as, and petiole of anal cell equal in length to anterior crossvein.

Holotype: Male, La Cholla, Sonora, V–30 '54 (D. K. Duncan), in the Cornell University Collection (via Charles H. Martin).

Laphystia texensis Curran

Laphystia texensis Curran 1931, Amer. Mus. Novitates No. 487: 15.

Described from three males and five females from Galveston, Texas, June 5, 1900 (W. M. Wheeler collection), in the American Museum of Natural History.

One paratype, and female specimens from the following localities, have been seen. TEXAS: Beach, 17 mi. W. Sabine Pass, VI–10 to 12 '56 (H. E. Evans, E. G. Matthews); Cameron Co., VIII–3 '28 (R. H. Beamer); Galveston, X–8 '32 (R. K. Fletcher); and Galveston Island, VIII–9. LOUISIANA: Cameron, VI–17 '48 (R. H. Beamer).

It seems possible that *texensis* is a variant of *opaca*.

Laphystia tolandi, new species

Male: Length 9 mm. Head black, densely white-pollinose; palpi and proboscis black. Hairs and bristles white, a single row of bristles on oral margin becoming double at the middle, hairs above proclinate and as long as first antennal joint, face at antennae equal to width of one eye. Antennae black, first joint slightly longer than second, two white bristles below on first, sparse hairs white; third subequal in length to first two; style one-fourth as long as third joint.

Mesonotum densely gray-pollinose, central stripe and intermediate area appearing black at some angles. Hairs and bristles white, hairs very short, appressed, with a few short, erect ones anteriorly; three presutural, three or four supraalar, and three postalar bristles, three or four posterior dorsocentral hairs. Pleura and coxae densely grayish-white-pollinose and white-haired. Scutellum densely gray-pollinose, narrow posterior margin at middle black, hairs on disc short, appressed, white; several short, erect hairs posteriorly, and four strong white marginal bristles.

Abdomen brown, becoming lighter apically, first segment and sides and posterior margins of segments 2 to 6 gray-pollinose, fasciae indented at the middle anteriorly on segments 1 to 4, very narrowly divided on 5, and narrowly divided on 6. Hairs white, longer on the sides of first segment, very short, appressed otherwise; bristles white, 3 to 6 on sides of each segment. Genitalia brownish black, hairs white. Venter wholly gray-pollinose, with sparse, erect, white hairs.

Legs brownish-black, narrow apices of femora and narrow base of tibiae yellowish-brown. Short appressed hairs white, bristles white. Claws black, basal one-third brown; empodia brown; pulvilli white, three-fifths as long as claws.

Halteres yellow, lower base brown; alulae yellow, narrow margin and fringe white. Wings hyaline, veins brown; anterior crossvein slightly before middle of discal cell; anal cell petiolate.

Female: Length 10 mm. Similar to male. Pollen of face, frons, mesonotum, and mesopleura with a golden cast. Six scutellar bristles. Pollinose fasciae entire on segments 1 to 6 but indented slightly at middle anteriorly, narrow segments 7 and 8 wholly gray-pollinose; small ovipositor brown, apical hairs and bristles white. Middle and hind femora lighter brown on basal one-third. Anterior crossvein slightly beyond middle of discal cell.

Holotype: Male, Lahontan Reservoir, Churchill Co., Nevada, VI–13 '49 (C. H. Martin). *Allotype:* Female, same data (J. Wilcox). *Paratypes:* 96 specimens, same data and VII–5 '58 (C. H. and Dorothy Martin, Guy F. Toland, and J. Wilcox). One female, Fish Springs, Juab Co., Utah, VII–2 '54 (R. D. Anderson).

This species varies from specimens which have the abdomen and legs almost wholly brownish black to those which have the abdomen largely and the basal two-thirds of the femora reddish-brown. In this species the marginal cell of the wings is closed and short-petiolate.

Laphystia torpida Hull

Laphystia torpida Hull 1958, Psyche 64(2): 70–72.

Type, female, Tracy, Calif. (San Joaquin Co.), VI–13 '49 (J. W. McSwain), University of California (Berkeley).

Male: Length 8 mm. Head black, densely gray-pollinose, face, frons, and vertex with a golden tinge. Hairs and bristles white, oral bristles and hairs about twice as long as the proclinate hairs on upper part of face. Antennae brown, first joint broader and 1⅓ times as long as second, both short white-haired, first with a strong, white bristle below; third subequal in length to first two; style narrow and about one-fourth as long as the third.

Mesonotum densely grayish-golden-pollinose, central bisected stripe evident at most angles, outside the central stripe there is a narrow bare stripe bisected by the transverse suture and outside these, posteriorly, narrow bare areas on each side. Hairs short, recumbent, yellow, with a few longer ones posteriorly. Bristles yellowish, two or three presutural, two or three supraalar and two postalar. Pleura and coxae densely yellowish-gray-pollinose, hairs white. Scutellum densely yellowish-gray-pollinose, narrow posterior margin

shining brown, dense recumbent, yellowish hairs on disc longer than those on the mesonotum; about 10 marginal hairs as long as first two antennal joints.

Abdomen dark brown, broad sides of segments 1 to 6 and posterior one-third of segments 2 to 6 yellowish-gray-pollinose. Short, recumbent hairs yellowish, with a few longer hairs on sides of first segment; bristles short, white, varying in number from 1 to 5. Venter yellowish-gray-pollinose and short, recumbent, yellowish-haired. Genitalia brown, with short white hairs.

Legs, including trochanters, brown, narrow apices of femora and narrow base of tibiae yellowish, femora thinly gray-pollinose; hairs and bristles yellowish-white; claws black, basal one-third reddish; pulvilli white, one-half length of claws; empodia brown.

Halteres yellow, base of stem brown. Wings hyaline, veins brown; anterior crossvein at one-third length of discal cell; petiole of anal cell as long as anterior crossvein.

Hypotype: Male, 2½ mi. N. of Davis, Calif., VII–26 '46 (E. Cott and R. Bohart), University of California (Davis).

Other specimens, same data, and Davis, Calif., VII–16 '46 (R. Bohart) and V–22 '57 (M. W. Stone, Itol J. and J. Wilcox); Dixon Rd. and 101, Milpitas (Santa Clara Co.), Calif., VI–29 '52 (D. J. Burdick); and Pittsburg, Calif., VI–12 '25 (S. W. Bromley).

This species has the shortest pulvilli, with the exception of ***martini*** new species.

Laphystia utahensis new species

Male: Length 7 mm. Head wholly white-pollinose, palpi and proboscis black; hairs and bristles white. First antennal joint brown, remainder yellowish-brown; hairs white, first joint with four or five white bristles below, slightly broader and about 1⅓ times as long as second; third joint subequal in length to the first two; style about one-fourth as long as third joint.

Mesonotum white-pollinose with a golden tinge, central stripe and intermediate area appearing darker at some angles. Hairs largely short, appressed, golden, anteriorly and posteriorly longer, erect, white. Bristles yellowish, two presutural, two supraalar, two postalar. Pleura and coxae densely grayish-pollinose, mesopleurae with a yellowish tinge; hairs white. Scutellum densely golden-pollinose and short-pilose, the sparse, erect discal and marginal hairs yellowish; apical margin at center bare of pollen.

Abdomen yellowish; segments 1 and 2 wholly white-pollinose, appearing yellowish; sides and posterior one-third of segments 3 to 6 yellowish-gray-pollinose, on segments 3 and 4 the pollen extends forward at the middle to the anterior margins and on segment 3 the anterior margin is narrowly pollinose; there is a suggestion of a median division on segment 5. Hairs short, appressed, golden, white and longer on lateral margins and on sides of segments 1 and 2; bristles pale yellowish, about three on each side of segments 1 and 4 to 6, and four or five on segments 2 and 3. Genitalia yellowish-brown, white-haired. Venter white-pollinose and sparsely white-haired.

Trochanters yellowish-brown; femora wholly, and tibiae except tips, yellowish; apices of tibiae, and the tarsi, brown; claws black, basal one-third reddish; pulvilli white, two-thirds as long as claws; hairs and bristles white. Fore and middle femora largely, and hind femora on dorsal half, whitish-pollinose.

Halteres pale yellow, base brown. Wings yellowish, veins light brown; anterior crossvein at one-third length of discal cell.

Female: Length 8 mm. Similar to male. Pollen of the head with a slight yellowish tinge. Only third antennal joint yellowish. Second abdominal segment with small spots on either side bare of pollen; segments 7 and 8 wholly pollinose; ovipositor brown. Anterior crossvein at four-ninths length of discal cell.

Holotype: male, St. George, Utah, 12 mi. N.E. Hwy. 17, V–23 '59 (J. Wilcox). *Allotype:* female, same data. *Paratypes:* 42 males and 37 females, same data, V–22 and 23 '59 (Itol J. and J. Wilcox); and one male, Palen, Utah (J. M. Aldrich), in the U.S.N.M. One female in rather poor condition, Gila Valley, Yuma, Ariz., swept alfalfa, VII–11 '56 (G. D. Butler), University of Arizona collection, is tentatively identified as this species. Our specimens were collected on the sandy banks of the Virgin River.

In some specimens there is a suggestion of a black spot at the tip of the dorsum of the fore and middle femora and the entire narrow dorsum of the hind femora are black. In a few female specimens the pollinose fasciae on segment 5 and rarely on segment 4 also are interrupted at the middle.

See note under *Laphystia howlandi*.

Laphystia varipes Curran

Laphystia varipes Curran 1931, Amer. Mus. Novitates No. 487: 15–16.

Holotype male and allotype female, Cherokee, Okla., Salt Plains, VI–16 '30 (R. D. Bird), in the American Museum of Natural History.

Specimens have been seen from the following localities. KANSAS: Clark Co., 1962 ft., June (F. H. Snow); Nickerson, VI–25 '36 (J. D. Beamer). NEW MEXICO: Santa Rosa, VI–23 '40 (D. E. Hardy). OKLAHOMA: Lugert, VI–11 '37 (Standish-Kaiser). TEXAS: Brownsville, June (F. H. Snow); Hidalgo Co., IX–8 '33 (S. W. Bromley); Laguna Madre, 25 mi. S.W. Harlingen, IV–10 '45 (D. E. Hardy, V. L. Wooley); Stephen F. Austin State Park, near Sealy, VI–14 to 16 '56 (H. E. Evans, E. G. Matthews).

This species has the basal one-half or more of the hind femora yellowish; the mesonotal hairs (except marginally) are very short, recumbent, and of brassy color; and there are no longer hairs on the third or following abdominal segments of males, or on the second or following segments of females. The pollinose fasciae on abdominal segments 2 to 5 are separated by about one-half the width of the abdomen. The scutellum has about 10 fine, erect, white, marginal hairs. The pulvilli are subequal to the claws in length.

Specimens placed here tentatively are a male and three females from near Grants, New Mexico, VII–4 '40 (B. Rotger, C. R.). The fasciae on the abdomen are separated at the middle as follows: male, first segment by one-half, segments 2 to 5 by one-fourth the width of the abdomen; females, first segment by one-third, segments 2 to 5 by two-ninths the width of the abdomen. The fascia on segment 6 is entire in both sexes.

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ELECTROGRAPHIC RECORDING OF FOREGUT ACTIVITY IN LARVAE OF GALLERIA MELLONELLA[1]

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ABSTRACT

In the technique used here for recording electrical activity associated with movements of the foregut, the larva was essentially intact but interfering activity of somatic musculature was blocked by specific paralyzants. The esophagus, crop, and proventriculus were found to be centers of activity. Simple pulsating contractions and peristaltic contractions both occurred. Electrograms of these contractions showed independent actions as characteristic waves, and integrated actions as complex tracings. Disorganized activity was recognized as such, but components could not be identified. As examples of pharmacologic action, serotinin and epinephrine stimulated peristaltic contractions in the crop. Carbon dioxide reversibly stopped any action, and under certain conditions DDT induced spasmodic contractions and regurgitation.

Two approaches have dominated the study of insect pharmacology and toxicology. One is a fragmenting approach; the action of chemicals on isolated systems is studied biochemically or physiologically. The other evaluates the gross results of chemical application in terms of mortality. Both approaches converge in purpose when results are interpreted as indirect measures of physiological events taking place in the intact animal.

The more direct study of integrated physiological events has largely been impractical be-

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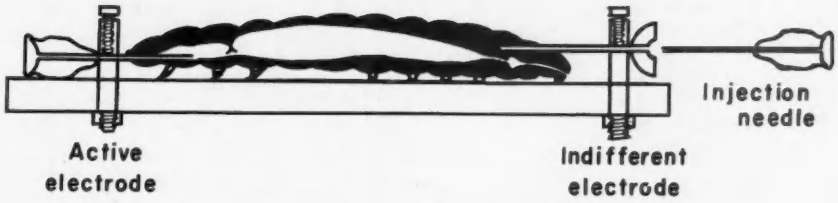


FIG. 1.—Sectional diagram of electrode assembly with larva in position for recording foregut activity.

cause (1) specific agents are not available for blocking interfering functions, and (2) the courses of functional change in target systems are difficult to follow in intact animals. This paper describes a technique applied to one physiological system in which these limitations are minimized. It is a method for studying the neuromuscular physiology and pharmacology of the foregut in the larva of the greater wax moth, *Galleria mellonella* (L.).

What little is known about the neuromuscular physiology of the foregut has been summarized by Day and Waterhouse (1953) and by Hoyle (1957). The observations of Yeager (1931) are particularly appropriate for comparison with those reported here.

MATERIALS AND METHODS

Larvae for use were reared in a medium consisting of a mixture of a proprietary infant cereal and dog meal moistened with honey. The largest available larvae were most suitable for experiment.

The recording technique depends upon the fact that muscular activity in the foregut, as elsewhere, is associated with electrical events that can be sensed by electrodes, and with suitable amplification, recorded by a pen-writing galvanometer.

Although a foregut electrogram can be made of an active larva, it is doubtful if the foregut physiology is any more independent of the activity of the somatic neuromuscular system, increased by the attempts of the larva to escape confinement, than it is of the decreased activity of this system under differential sedation. So, an important feature of this technique is the use of agents which inactivate the body wall muscles but not the foregut. The innervation of the foregut may or may not be affected by the three blocking agents used, but this aspect of the inquiry will not be discussed in this paper. One useful blocking agent is the venom of the wasp *Microbracon hebetor* Say (=*Habrobracon juglandis* Ashmead). This is a potent inhibitor of somatic muscular activity in *Galleria* larvae; presumably it blocks the neuromuscular junction (Beard 1952). The larva can be paralyzed either by a direct sting or by injection of filtered water extracts of the wasps. The result is a flaccid larva in which the heart, gut, and nerves are functional. A similarly appearing larva, in which a neural block is believed to be more central than at the neuromuscular junction, can be obtained with the venom of the spider *Theridion tepidariorum* (Koch). Nicotine also differentially affects the somatic and visceral neuromuscular systems and effectively paralyzes, reversibly, the somatic musculature.

The insect larva, essentially intact except for its muscular inactivation, can be positioned on an electrode stage and readied for chemical injection or exposure to vapors without dissection. This means that the preparation requires no attention, and observations can be mad on the same insect for a period of several days The electrode assembly (figure 1) consists of two electrodes, separated by about the length of a larva, mounted in binding posts that re secureda in a plastic block. This block is mounted on a mechanical stage to provide well-controlled movement in the axis of the larva. The active electrode is a dulled 30-gauge hypodermic needle, which can pass between the mouth parts and into the lumen of the foregut without injury. The other, indifferent, electrode is a shortened needle and shank of a 23-gauge hypodermic needle. Leads from the electrodes go to a Grass P4 preamplifier. A power amplifier and a recording galvanometer from a Grass electroencephalograph complete the sytem.

The larva is placed by gently slipping the head and first thoracic segment over the active electrode. Impaling the integument of a posterior segment over the indifferent electrode causes the only mechanical injury. This is self-sealing, and practically no blood is lost. The lumen of the indifferent electrode provides a channel into the body cavity through which a 30-gauge hypodermic needle can pass for injections without further mechanical injury. The injection device, consisting of a hypodermic syringe activated by a micrometer screw, is rigidly held so that its needle is coaxial with the indifferent electrode. This being rigid, and the insect electrode assembly being movable in the same axis, the tip of the injection needle can be introduced into the insect's body cavity quickly and without sig-

nificantly disturbing the recording. This separation of the injection system from the recording system has the principal advantages that a precise dose of chemical can be introduced at a specific time without seepage effects and that different chemicals can be introduced in sequence without disturbing the continuity of recording. Injection of chemicals can be made directly into the foregut by using a syringe attached to the active electrode. In this instance, the syringe

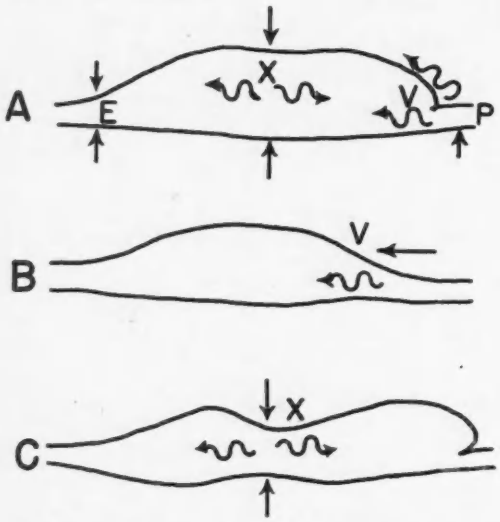


FIG. 2.—A, Diagram of foregut indicating activity centers at E (esophagus), X (crop-anterior proventriculus), V (posterior proventriculus), and P (proventriculur constriction). B, Diagram of change of shape of foregut as the V contraction progresses. C, Diagram of change of shape of foregut as the X contraction progresses.

must be fixed in place as a part of the recording system, so only one chemical can be introduced into the gut of a single preparation. With the particular device used, there is less control of quantity injected than is the case with the body cavity injection. These limitations are imposed by the fact that a 23-gauge needle is too large to introduce between the mouth parts. Hence a channel into the gut cannot be provided for a movable needle. The electrode stage can be enclosed by a plastic cover with openings for the circulation of gases or toxic vapors. In this way materials administered via the tracheal system can be tested.

A wax dish under the positioned larva simplifies dissection, which makes possible the relating of gut movement with the electrical record. The characteristic movements of the exposed foregut can be observed at the same time an electrical record is made. In this way it has been possible to observe activity representing almost all types of records that have been obtained. These are the records presented in the next section. The types of activity are sufficiently characteristic that foregut movement in the intact larva can now be visualized by observation of the electrical record alone. This is a great advantage, as dissection often disrupts or modifies foregut activity.

RESULTS AND DISCUSSION

Observation of the exposed foregut discloses three centers of activity with several distinctive types that may be independent or integrated (figure 2). These yield a variety of electrograms as will be discussed. A few other electrographic records have been obtained which at present cannot be identified with muscular response. They may be electrical artifacts, excitatory phenomena without mechanical movements, or integrated activity in which the components cannot be segregated.

Yeager (1931) reported on the activity in the foregut of *Periplaneta fuliginosa* (Serv.) as including peristaltic, antiperistaltic[2], and pulsatory contractions in the crop and contractions in the gizzard. Basically, these activities as described are not too different from those in *Galleria*. Interactions of these centers become apparent in electrograms.

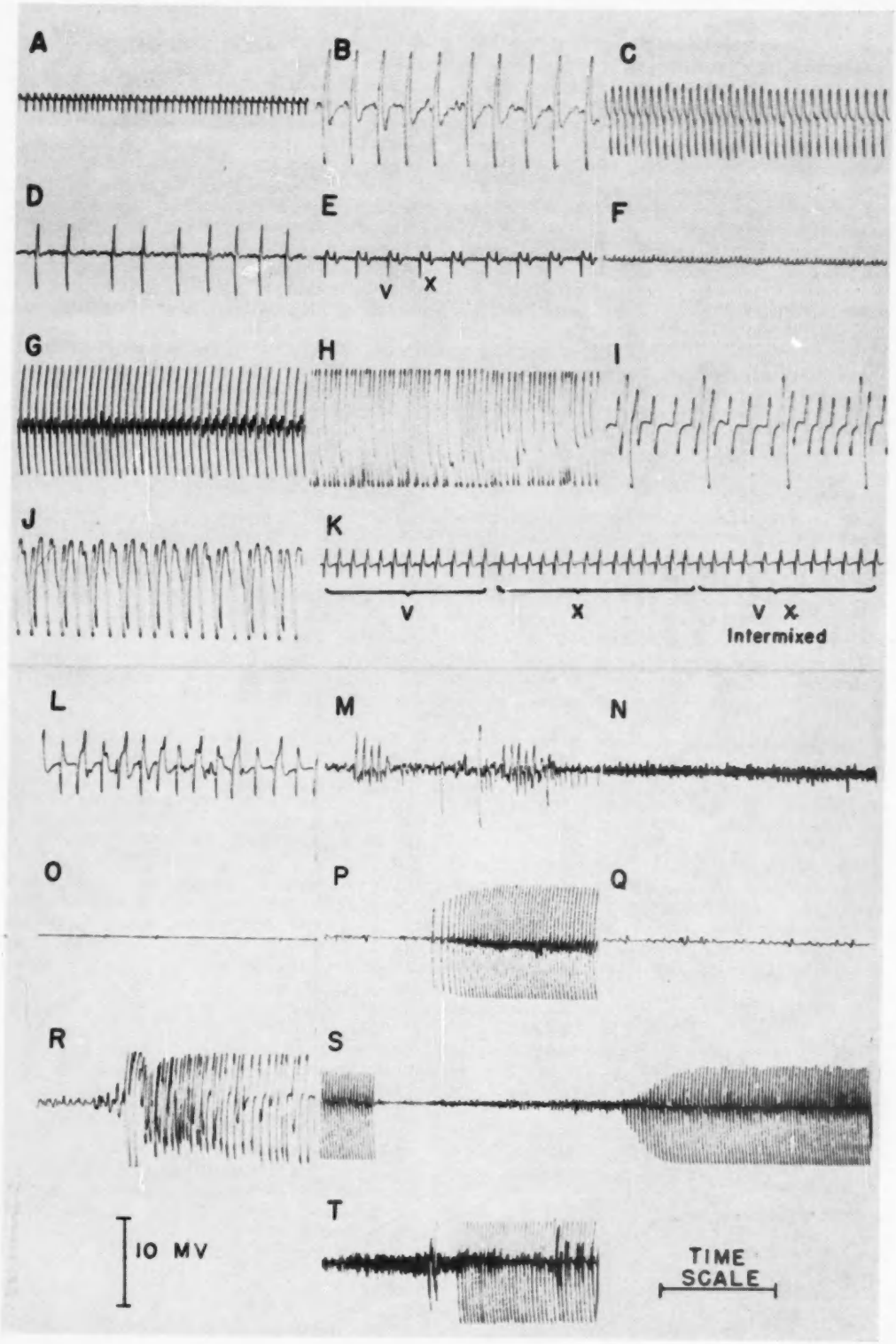
Bittner (1954 has described portions of the foregut of *Galleria* larvae. He considers the anterior portion of the prominent sac-like region to be the crop, the rest being the proventriculus. This view is followed here. Of these regions, the

[2]Although the term "antiperistalsis" has been commonly used as indicating reverse peristalsis, it can be ambiguous and inappropriate. An anteriorly directed peristaltic wave may be perfectly normal and characteristic and can be considered reversed peristalsis only in the sense of the popular belief that peristalsis ought to be posteriorly directed. Peristalsis is peristalsis, regardless of direction; it becomes reversed when the point of origin shifts and the wave moves in the opposite direction. The term "antiperistalsis" might better be reserved for forces that oppose peristalsis, regardless of direction.

EXPLANATION OF FIGURE

FIG. 3.—Electrograms of foregut activity. The time scale indicates 12 seconds in B, I, and J; 24 seconds in K, L, and R; and 60 seconds in all other records. In I, the upstroke indicates increasing negativity inside the foregut with respect to the body cavity, the downstroke increasing postivity. In all other records the downstroke indicates increasing negativity, the upstroke increasing positivity. For further explanation see text.

FIGURE 3



proventriculus is the most sensitive center of activity. The proventricular constriction anterior to the midgut may contract in pulsatory fashion. The pulsation registers as a predominantly monophasic signal, usually of less than one millivolt (figure 3, A). The pulses may be as rapid as two or three per second, but the frequency varies considerably. At times they are exceptionally rhythmic; at other times they are irregular. For convenience in discussion, this proventricular pulsation is symbolized by "P."

Originating at the posterior proventriculus, an independent, propagated peristaltic wave may occupy the whole proventriculus, spreading forward and dissipating at the constriction that marks the junction of the crop and proventriculus. This anteriorly directed peristaltic wave going to completion registers as a strong diphasic signal, sometimes exceeding 10 millivolts (figure 3, B). An incompleted wave registers similarly, but with reduced signal strength (figure 3, C, D, E). This type of contraction is symbolized as "V," suggesting that it is a spreading wave originating at one point.

The V contraction may be highly rhythmic (figure 3, C) or intermittent (figure 3, D). Both visibly and electrographically the P contraction and a partial contraction of V may at times be indistinguishable, as the area involved is small. Perhaps neurological and pharmacological study will suggest better differentiation.

The crop-proventricular region is the center of a somewhat different action. When at a minimum it is a simple constricting contraction, but with greater strength it proceeds posteriorly as a strong peristaltic wave and also from the same origin it simultaneously spreads anteriorly as a weaker peristalsis. It is possible that these peristaltic waves are not truly propagated and so are illusory because the strong constricting action affects a large portion of the crop. This action, symbolized by "X," also accompanies a strong diphasic signal. Unfortunately for diagnostic purposes, its electrogram cannot always be distinguished from the V contraction wave (figure 3, K). At times, the polarities are opposite (figure 3, E), but more often they are the same.

Pulsating contractions occur in the esophageal region. Designated as "E," these have not been positively identified in electrograms. In one possible instance, a weak, monophasic signal, opposite in polarity to that usually seen, was observed when the esophageal region was pulsating (figure 3, F). Slight pulsations were also occurring in the proventriculus, which may have been the source of the signal. Limiting the active electrode to the esophageal region does not augment the E signal. It is believed that the E signal is too weak to be distinctive in the electrographic recordings, but it may contribute to irregularities of low amplitude.

Interactions of these independent components are responsible for a variety of complex electrograms. Perhaps the most common integrated activity is a combination of the X and V waves. The completion of the V wave appears to trigger the X wave, and possibly vice versa. The result is a rhythmic alternation of the two waves, about equal in strength. This produces a kneading action that should effectively mix the contents of the foregut (figure 2, B, C). The electrogram shows a succession of strong, uniform, diphasic waves, each separated by a momentary, ill-defined irregularity (figure 3, G). Under certain abnormal conditions, as with nicotine or other stimulation, the contraction phase of X coincides with the relaxation phase of V, and the contraction phase of V coincides with the relaxation phase of X to give a succession of especially strong diphasic signals with little or no break between waves (figure 3, H). If the X and V waves are essentially independent, acting at different rates and amplitudes, but not in conflict, the electrogram clearly shows the two components (figure 3, I).

The V and X waves may be synchronized at ratios different from 1:1. Figure 3, J, shows a ratio of 2:1. A different type of synchrony is shown in figure 3, K. A series of V contractions alone was followed by a series of X contractions alone. These in turn, were followed by a series of V and X contractions intermixed without order. No break appears in the record and the two waves cannot be distinguished. The differences were apparent only by direct observation of the exposed crop.

If the V and X contractions are in conflict—sometimes independent, sometimes reinforcing or antagonizing each other—the waves of the electrogram are irregular and the components cannot be identified (figure 3, L). If a third component, the P contraction, is present with X and V uncoordinated, the electrogram is still more confusing (figure 3, M). If this erratic record is of low amplitude, slight contractions at any of the centers of activity, or localized twitchings elsewhere may be responsible (figure 3, N). In the absence of activity, the electrograph records a straight line (figure 3, O). This, of course, could represent a completely inactive foregut, or one incapable of activity. The competency of the foregut can be challenged by the injection of serotonin (5-hydroxytryptamine), which has a marked stimulatory action, primarily on the V wave (figure 3, P).

In the complete absence of other activity, an irregular trace of low amplitude (figure 3, Q) may be suspect, as this record can be obtained when the active electrode punctures the gut, thus shorting out activity signals. This, too, can be challenged by serotonin.

One dramatic action can logically be expected, but has not been seen nor knowingly recorded.

This is that associated with the relaxation of the proventricular valve and the propulsion of food into the mid-gut. This probably occurs infrequently and presumably is of limited duration, but it must happen. The electrogram of this action, however, cannot be visualized at present.

An account of chemical action on the neuromuscular physiology of the crop cannot be given at this time. The action of serotonin has already been indicated, and three other examples illustrate the application of this technique to pharmacological study. Under certain conditions the effect of DDT is to induce regurgitation in *Galleria* larvae (Beard 1958). At the moment of regurgitation, the crop contracts forceably and spasmodically, being recorded as in figure 3, R. The proventriculus is richly tracheated and so is quickly responsive to gases which affect it. This is evident in figure 3, S, a record obtained when carbon dioxide was introduced into the enclosure around a test larva. Inactivity was promptly induced, but recovery quickly followed the removal of the carbon dioxide from the environment. Epinephrine has a stimulatory action similar to that of serotonin. This is illustrated in figure 3, T.

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STUDIES ON TOTAL BLOOD CELL COUNTS OF THE SOUTHERN ARMYWORM LARVA, PRODENIA ERIDANIA (LEPIDOPTERA)[1]

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ABSTRACT

When blood cells of sixth-stage *Prodenia eridania* larvae were prevented from clumping by treatment with warm acetic acid vapors, fixation in hot water, or injection of nucleic acid, the number normally ranged from ca. 17,000 to 45,000, with a mean of about 28,000 per cu. mm. If clumping was not prevented, at least 38% of the cells were not available for estimation. Normal total hemocyte counts were found after injection of foreign material (trypan blue, India ink, and *Bacillus subtilis*), after starvation for 70 hours at 4° C., after ligaturing of the head or anus, and in grossly unhealthy larvae from moribund cultures. Starvation at room temperature led to desiccation of *Prodenia* larvae, and to a qualitative decrease in the blood volume, and therefore to an increase in number of cells per cu. mm. It is suggested, however, that the absolute number of cells in the animal remained the same. The number of blood cells was greatly reduced in larvae having a naturally occurring bacteremia. On the basis of these findings the blood cells of *Prodenia eridania* seemed not to constitute a particularly effective system for the defense of the organism.

In many insects the blood cells rapidly clump together in freshly drawn blood (e.g., Oriental cockroach, Yeager and Knight 1933), in others only the plasma coagulates (e.g., Japanese beetle grubs, Beard 1950), whereas in still others neither clumping of cells nor plasma coagulation occurs (e.g., the honey bee larva, Yeager and Knight 1933. Estimates of blood cells per cubic millimeter of hemolymph (i.e., total hemocyte counts) from various intact insects have principally been made either (1) without treatment (Tauber and Yeager 1934; Jones 1956; and Lhoste 1957), (2) after dilution of fresh blood drops in a suitable diluent (Yeager and Tauber 1933), (3) subsequent to injection of nucleic acid (Paillot 1923), (4) after exposure to hot fatty acid vapors, generally acetic acid (Shull et al. 1932; Fisher 1935; Shull 1936; Webley 1951; and Arnold 1952), and (5) following fixation of the whole insect in hot water (Yeager 1945; Jones and Tauber 1951). A variety of other valuable methods for preventing coagulation of the blood are available now (Beard 1950; Grégoire 1953), but they have not

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Table 1.—Total hemocyte counts of unfixed and heat-fixed sixth-instar *Prodena eridania* (Cram.)

Length (mm.)	Untreated larvae			Heat-fixed larvae		
	No. used	Mean	Range	No. used	Mean	Range
22	6	12,840	9,040–18,320	—	—	—
25	4	19,990	17,120–25,440	11	32,144	22,560–44,800
28	—	—	—	9	27,449	19,520–43,360
30	5	22,708	19,200–29,360	10	25,144	20,240–34,600
32	5	17,440	12,440–23,720	19	27,440	16,920–42,320
33–34	9	17,451	13,480–27,280	—	—	—
35	11	12,682	9,040–20,240	13	26,494	20,960–33,220
		17,185±1,671			27,734±1,400	

yet been used for studying total blood cell counts in insects.

In the present investigation total hemocyte counts of sixth-stage larvae of *Prodenia eridania* have been made after no fixation, heat fixation, chilling, following exposure to acetic acid vapors, ether, and chloroform, and subsequent to the injection of nucleic acid, so that these methods might be evaluated in an insect in which plasma coagulation is absent (Babers 1938), and blood cell clumping *in vitro* is very marked. The most consistent of these methods was then used to study the effects of injections of bacteria, trypan blue, and India ink, as well as the effects of starvation, desiccation, and ligation on the number of blood cells per cubic millimeter.

METHODS

Eggs of the southern armyworm, *Prodenia eridania* (Cram.), (Lepidoptera) were placed on a piece of fresh lettuce in a petri dish and allowed to hatch at 25° to 27° C. When the larvae were 5 to 6 days old (approximately 10 mm. long), they were transferred into either large cylindrical glass mouse jars (6″ x 8″) with cheesecloth tops and paper-towel floors, or into stainless steel chambers (12″ x 21″ x 14″) with hinged, fine copper wire screen mesh tops, having sawdust floors. Both rearing chambers were provided with fresh kale daily. Before pupation, larvae in the mouse jars were removed to the larger metal chambers. Five percent sucrose on absorbent facial tissue in petri dishes was available to adult moths and was replenished daily. Spiral strips of waxed paper were placed in cages for oviposition.

Larvae were exposed to acetic acid, ether, or chloroform vapors in a screw-cap glass tube that had a fine copper wire screen over a cotton pellet freshly saturated with the given compound. For heat fixation, larvae were plunged into a hot water bath held at various constant temperatures. Groups of 10 larvae were starved in large glass beakers having absorbent paper towel floors. In ligaturing experiments, larvae were tied with light, soft, four-ply cotton twine. Injections were made through the dorsal surface of the fourth or fifth abdominal segment, with a fine needle attached to a plastic syringe graduated to 0.02 ml.

Only sixth-instars measuring 22 to 35 mm. in length were used and, unless specified differently, they were well-fed and healthy looking.

In making total counts, the prolegs were cut off with fine pointed scissors, and three or four drops of pale greenish or yellowish blood allowed to flow onto a clean glass slide. A portion of the blood was quickly drawn to the 0.5 mark of a Thoma white blood-cell diluting pipette, the tip carefully wiped clean, and the blood then diluted to the 11 mark with a physiological saline (NaCl 0.9 g., Kcl 0.042 g., $CaCl_2$ 0.048 g., $NaHCO_3$ 0.002 g. distilled water 100 ml.) containing acetic acid (1%).

Using a Levy double-line hemocytometer with improved Neubauer ruling, cells were counted in the four corner and central squares, and the sum multiplied by a factor of 40 to give the number of cells per cubic millimeter. If the cells clumped or were otherwise unevenly distributed in the chamber, the preparation was discarded.

RESULTS

Hemocytes in a drop of freshly drawn blood on glass or paraffin coated surfaces rapidly agglutinated. The cells readily adhered to glass. If diluted with Wyatt's medium (Wyatt 1956), the cells migrated and often formed elaborate syncytia in 3 to 5 hours at 25° and 35° C. Clumping of unfixed cells was greatly accelerated by mechanical agitation (e.g., by gently rocking the slide). If a needle was drawn through a fresh blood drop it left tracks of clumped cells along its path. By stirring the drop, one could pick up with a needle a mass of the whitish blood cells. Dilution of unfixed blood two to three times with physiological saline did not prevent cell clumping, but addition of acetic acid (1%) or formaldehyde (4%) to the diluent definitely reduced the degree of agglutination. Clumping was completely prevented by fixing whole larvae at either 55° or 60° C. for 1 minute; it was not prevented, however, at 50° C. for 1 to 5 minutes. Cells vigorously agglutinated in either etherized or chloroformed larvae (5 to 30 minute exposures)

at room temperature. Once the blood cells were clumped, neither cold nor hot tryspin would disperse them.

Total blood cell counts from 40 unfixed *Prodenia* larvae ranged from ca. 9,000 to ca. 29,000 cells per cu. mm., a 3.2-fold variation (overall mean, 17,185 ± 1,671). In many cases, if clumping was not prevented, the pipettes rapidly clogged so that counts could not be made at all. Eleven larvae exposed to glacial acetic vapors for 5 minutes at 25° C. had counts ranging from ca. 11,000 to ca. 26,000 cells per cu. mm. (mean 18,507 ± 1,338). Injection of 0.01 ml. of 2% nucleic acid in Wyatt's medium did not uniformly prevent the cells from clumping, but injection of 0.02 ml. did. Total counts made on the latter averaged ca. 19,000 cells per cu. mm. (range 13,200 to 37,600), without taking into account the injected fluid, which very probably accounted for the slightly lower-than-normal count. Five larvae chilled for 1 minute in an ice bath had a mean count of 23,245 cells per cu. mm. (17,760 to 25,760). Excessive blood cell clumping occurred in larvae placed at —20° C. for 10 minutes.

Sixty-two *Prodenia* fixed in hot water at 60° C. for 1 minute had individual counts that ranged from ca. 17,000 to ca. 45,000 cells per cu. mm. (overall mean, 27,734 ± 1,400). When 14 larvae were exposed to acetic acid vapors for 45 minutes at 35° C. individual total hemocyte counts ranged from ca. 19,000 to ca. 39,000 cells per cu. mm. (mean 27,471, ± 443). In our experience heat fixation was preferable to acetic vapor since it was simple, easy, very rapid, and did not cause excessive regurgitation.

Mean total hemocyte counts of heat-fixed *Prodenia* varied from ca. 25,000 to ca. 32,000 cells per cu. mm. during the sixth stadium, i.e., there was no evident trend in their number as they approached pupation (table 1). *Heat-fixed larvae were used for all subsequent studies.*

One to six hours after injection of 0.01 ml. of 0.5% trypan blue in Wyatt's medium (Wyatt 1956), the total count decreased by ca. 9,000 to ca. 13,000 cells, but returned to a normal mean of 21,200 by 24 hours. Controls injected with Wyatt's medium alone showed no basic change in total counts after 1 and 6 hours, but decreased slightly at 24 hours. Injection of India ink did not alter the total count in 4 hours. A heavy suspension of *Bacillus subtilis* (0.1 ml. of culture broth diluted with 0.9 ml. of Wyatt's medium) had not changed the normal number of circulating blood cells after 24 hours (mean count 21,560 cells per cu. mm.). However, during the course of the study four larvae were found to be naturally infected with bacteria (type not identified): these larvae had greatly lowered total counts (mean 8,370 cells per cu. mm., range 4,800 to 13,000).

Overcrowding cultures of young *Prodenia* very often led to high mortality. Prior to death such larvae became inactive, and had darkened thoraces and flaccid bodies. Blood removed from these worms was brownish in color rather than the normal pale green or yellow. The average total count on five obviously unhealthy larvae was normal (mean, 23,080 cells per cu. mm.).

At 25° C. starved *Prodenia* larvae visibly decreased in size (50% of the larvae shrunken at 48 hours, all shrunken at 72 hours), and available blood was qualitatively reduced. Since total counts on these worms had steadily increased with time of starvation (up to 113,000 cells per cu. mm. at 72 hours), and since this appeared to be correlated with the visible decrease in total blood volume due to desiccation, counts were made on larvae starved at 4° C. for 72 hours. Such chilled, fasting larvae did not show a decrease in blood volume, did not become desiccated, and were found to have normal mean total counts (mean, 22,300 cells per cu. mm.). Thus, starvation itself was not responsible for the increase in blood cells. Larvae with the tip of the abdomen ligatured did not become desiccated at room temperature and had a normal mean count of ca. 31,000 cells per cu. mm. at 24 hours, and a mean of 27,000 cells per cu. mm. at 48 hours.

No definite change in the relative number of circulating blood cells was found in head-ligatured *Prodenia* larvae (32 mm. long) at 17 hours (mean 28,760 cells per cu. mm.) or at 70 hours (mean 24,600 cells per cu. mm.), even on dry paper toweling. Somewhat elevated but still normal total counts were found at 24 hours (34,204 cells per cu. mm.) and at 48 hours (38,804 cells per cu. mm.). Worms with ligatured thoraces also had elevated but normal counts (33,000 cells per cu. mm.) at 24 hours and 31,500 cells per cu. mm. at 48 hours.

The various experiments on total cell counts of heat-fixed *Prodenia* larvae are summarized in table 2.

DISCUSSION

Most (85%) heat-fixed, normal, sixth-instar *Prodenia* used in this study had total blood cell counts ranging from 20,000 to 35,000 cells per cu. mm.[2], although 5% of them had counts lower than this range, and 10% had higher counts. The extreme individual variation was, however, only 2.7-fold, i.e., from 16,640 to 44,800 cells per cu. mm. These values are much more uniform than those reported for several other insects, e.g., in the American cockroach individuals vary as much as 4-fold (Smith 1938), in the mealworm, the mean normal variation is 5.3-fold (Jones and Tauber 1951), and in the field cricket the extreme variation is 18.3-fold (Tauber and Yeager 1934). If *Prodenia* are not fixed prior to making total counts, then approximately 38%

[2]Babers (1938) reported a range of 23,800 to 36,600 cells per cu. mm. (mean, 30,500) for 12 normal, heat-fixed (?) *Prodenia* larvae.

Table 2.—Summary of experiments on total hemocyte counts of heat-fixed, 32-mm. sixth-instar *Prodenia eridania* (Cram.).

Treatment	Hours after treatment when examined	No. used	Cells per cu. mm.	
			Mean	Range
Injected with 0.5% trypan blue in Wyatt's medium	1	10	14,640	6,320–19,920
	6	5	18,360	16,080–20,560
	24	9	21,200[a]	4,520–52,320
Injected with Bacillus subtilis broth diluted 1:10 with Wyatt's medium	24	10	23,240[a]	13,760–32,680
Injected with Wyatt's medium	1	10	22,240[a]	12,480–42,600
	6	6	30,240[a]	20,680–33,960
	24	8	18,720	14,480–28,400
Starved on dry paper towels at 25° C.	17	5	30,024[a]	26,200–35,360
	24	10	42,204	22,160–66,960
	48	10	58,220	26,560–122,360
	72	10	67,104	23,080–113,040
Starved on moist paper towels at 25° C.	70	5	46,000	37,120–54,160
Starved on moist paper towels at 4° C.	70	5	21,680[a]	16,080–27,840
Starved on dry paper towels at 4° C.	72	5	20,320[a]	19,320–20,960
Ligatured head; 25° C.; kept on dry towels	17	5	28,760[a]	24,560–31,960
	24	10	34,204[a]	17,600–60,520
	48	10	38,804	31,960–53,560
on moist towels	70	5	24,600[a]	18,080–33,240
Thorax ligatured; 25° C.; dry paper towels	24	7	33,000[a]	26,760–45,840
	48	10	31,500[a]	20,160–52,680
Tip of abdomen ligatured; 25° C.; dry paper towels	24	7	30,680[a]	19,120–4, 200
	48	10	27,240[a]	22,560–32,160

[a]Normal counts

of their blood cells are rendered unavailable through clumping. Even so, the total counts from unfixed worms were not lowered nearly as much as had been anticipated, very probably because counts could not be made from larvae where clumping was excessive.

Heat-fixed, trypan blue-injected larvae had significantly lowered total blood cell counts 1 and 6 hours after injection, unlike the controls. What happens to blood cells that temporarily leave the circulation is unknown but presumably they adhere to tissue surfaces. A reduction in blood volume without any change in the absolute number of circulating blood cells (i.e., the number of cells in the entire animal) during desiccation could explain the very high counts obtained at 48 and 72 hours. Yeager and Munson (1950) found that fasted and desiccated roaches still had the same blood volume in relation to body weight.

The number of blood cells circulating in *Prodenia* is clearly unaffected by a variety of experimental conditions. Even in grossly unhealthy larvae the total cell count is normal. Lowest counts were found in larvae naturally infected with bacteria, which is in agreement with a similar finding by Babers (1938).

From the experiments reported in this paper, it is evident that the blood cells of *Prodenia*, like those of the mealworm, do not actively respond to some presumably drastic emergencies. During the many physiological changes that must be occurring prior to pupation, the number of blood cells remains strikingly constant in spite of some complex changes in the various types of cells (see Yeager 1945). Arnold (1952) also found relatively little change in the total hemocyte count of last-stage larvae of the Mediterranean flour moth (the number of cells increased less just prior to pupation than during any earlier larval stage). In *Sarcophaga* larvae, on the other hand, the total number of circulating cells greatly increases just before pupation begins and then falls precipitously (Jones 1956).

One could expect blood cells to increase either in number or in power of phagocytosis or both when foreign material is injected into the hemocoel, if they are dynamically to protect the insect. The blood cells of *Prodenia* either showed no change in number or else markedly decreased with bacteremia. No change in number could indicate that the available blood cells already were sufficient to cope with the bacteria, there being no need for an increase. Or, it could indicate that the available blood cells were all in circulation, and that either no discrete hemocytopoietic tissues existed or that hypothetical hemocytopoietic

tissues or the circulating cells themselves were not stimulated by bacteremia. Since naturally occurring bacteremia produced a severe hemocytopenia, we are inclined to believe that the blood cells of *Prodenia* are unable to increase very much in total numbers: i.e., they are all, or nearly all, in circulation, and that the mitotic mechanism within certain circulating cells is probably either not stimulated or is insufficient to overcome the progressive destruction of blood cells. It would be of considerable interest to know what changes, if any, would occur in the total blood cell count if severely infected larvae were treated with suitable antibiotics.

As many as 85% of the blood cells of sixth-stage *Prodenia* larvae contain glycogen (Yeager and Munson 1941). These deposits disappear during starvation (loc. cit.). If it is true that the blood cell population remains the same when the volume of blood obviously diminishes, then the blood cells themselves are not being destroyed to provide food for other tissues in the larvae, nor are they transforming into other types of tissue cells.

The total number of circulating blood cells in *Prodenia* larvae is evidently not a good indication of the general state of health, since normal counts were obtained in grossly unhealthy animals. Certainly the blood cell population did not increase following a variety of experimental conditions, but tended either to remain constant or to decrease. The constancy could mean that they were either sufficient or resistant to demands made upon them. Their failure to increase during bacteremia suggests that they do not constitute a very formidable defense system against massive bacterial invasions.

ACKNOWLEDGMENTS

We are grateful to Dr. William L. Pond of the Laboratory of Tropical Virology for many kindnesses, including the facilities for this study. We have benefited from the critical reading of the manuscript by Dr. J. Franklin Yeager of the National Institutes of Health, and by Dr. William E. Bickley of the Department of Entomology, University of Maryland.

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PARACACOXENUS, NEW GENUS, WITH NOTES ON CACOXENUS INDAGATOR LOEW (DIPTERA: DROSOPHILIDAE)[1]

D. ELMO HARDY[2] AND MARSHALL R. WHEELER[3]

ABSTRACT

Cacoxenus Loew is redefined on the basis of the type species, *C. indagator*, which is redescribed (including characteristics of the genitalia) and for which a lectotype is selected. **PARACACOXENUS** Hardy, type *P. guttatus* Hardy and Wheeler (Washington and Oregon), is allied to *Cacoxenus*, *Gitona*, and *Gitonides*.

In studying the affinities of *Gitonides perspicax* Knab from Hawaii, comparisons were made with several species of *Gitona*, with the European *Cacoxenus indagator*, and with the undescribed species of *Cacoxenus* reported from North America by Wheeler (1952). These studies have shown that *Gitonides* and *Cacoxenus* are distinct, and that the American form is generically distinct from both of them. In addition to describing it as a new genus and species, we also take this occasion to report on the type series of *indagator*, the type species of *Cacoxenus*.

Cacoxenus Loew

1858. Weiner Ent. Monatschr. 2: 216. Type species: *C. indagator* Loew, by monotypy.

The genus was located in the Agromyzidae by Becker, and in the Milichiidae by Loew and Schiner. Collin (1911) pointed out that it could not possibly belong to the Agromyzidae, saying, ". . . it seems to resemble in many ways the genera at the commencement of the Drosophilidae such as *Acletoxenus*, *Leucophenga* and *Phortica*, and may ultimately have to be located there, but at present I leave it in the Milichiidae. . . ." Kröber (1912) assigned the synonymous *Paragitona* to the Drosophilidae, and Hendel (1917) placed *Cacoxenus* in the Drosophilidae. This arrangement has been followed by Duda (1924, 1926, 1934) and later authors.

Cacoxenus is clearly a drosophilid, related to *Gitona* and *Gitonides*, all of which possess strong prescutellar bristles, small postverticals, divergent basal scutellars, bare or rarely short-plumose aristae, and small sutural bristles. The described species are as follows:

Cacoxenus indagator Loew 1858, Weiner ent. Monatschr. 2: 218. This has been reported from a number of European localities, but comparisons of the male genitalia of the type series with specimens from Great Britain and Germany indicate that several species may be going under this name.

Cacoxenus semiluteus Loew 1869, Berliner ent. Zeitschr. 13: 51. Loew described this species from Cuba, placing it in the Agromyzidae. Wheeler (1952) has indicated that this is probably not a drosophilid.

Cacoxenus obscurus (Kröber 1912), Zeitschr. wiss. Insektenbiol. 8: 235. Originally described as *Paragitona obscura*. Kröber later published a note in the same volume (p. 329) making *Paragitona* a synonym of *Cacoxenus*, and *obscura* a synonym of *indagator*. The type should be re-examined before accepting this synonymy.

Cacoxenus exiguus Duda 1924, Arch. Naturgesch. 90A(3): 225. Reported only from Silesia.

Cacoxenus punctatus Duda 1924, op. cit. 225. Described from Formosa. The present status of this species is uncertain. Duda (1926) used the combination "*Phortica* (*Cacoxenus*) *punctatus*," making *Cacoxenus* a subgenus of *Phortica* Schiner, but later (1934) he treated *Cacoxenus* as a valid genus. Hendel (1933) placed *punctatus* as a synonym of *Gitonides perspicax* Knab, but Hennig (1941) retained it as a valid species of *Cacoxenus*.

Cacoxenus argyreator Frey 1932, Notul. Ent. 12: 84. Known only from Finland and Norway.

Cacoxenus inquilinus Hendel 1933, Deutsch. ent. Zeitschr. 1933: 46. Known only from Australia.

Cacoxenus indagator Loew

(Figs. 1a-c)

The senior author has had an opportunity to study a good series of specimens of this, the type species, thanks to loans made by Harold Oldroyd, British Museum (Natural History), Willi Hennig, Deutsches Entomologisches Institut, Berlin, and Fritz Peus, Zoological Museum, Berlin. Loew's cotype series, consisting of one male and two females labelled "Silesia, 5, 1858 (H. Loew)" was received from Dr. Peus. The male specimen bearing the name label in Loew's handwriting has now been designated as the lectotype and is located in the Zoological Museum, Humboldt University, Berlin.

The description given by Duda (1934) appears to be adequate except that the statement "*a. r. orb dicht hinter den p. orb*" does not seem to be correct since the anterior reclinate bristle is placed

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well behind the proclinate one, about one-third to two-fifths the distance between the proclinate and the posterior reclinate bristles (fig. 1a).

The following description, including the male genitalial characters which have not been described or figured, supplements that of Duda.

The front of the male is predominantly opaque black, lightly gray pollinose; it is about one-half longer than wide and is slightly narrowed anteriorly. In the female the front is distinctly gray pollinose and is about one-third longer than wide. The thorax is rather densely gray pollinose, the mesonotum very densely setose with 15 to 20 irregular rows of acrostichal setae. Each sternopleuron has a strong posteroventral bristle and several inconspicuous hairs arranged in a vertical row. Duda's wing figure is good; however, in the specimens examined the last

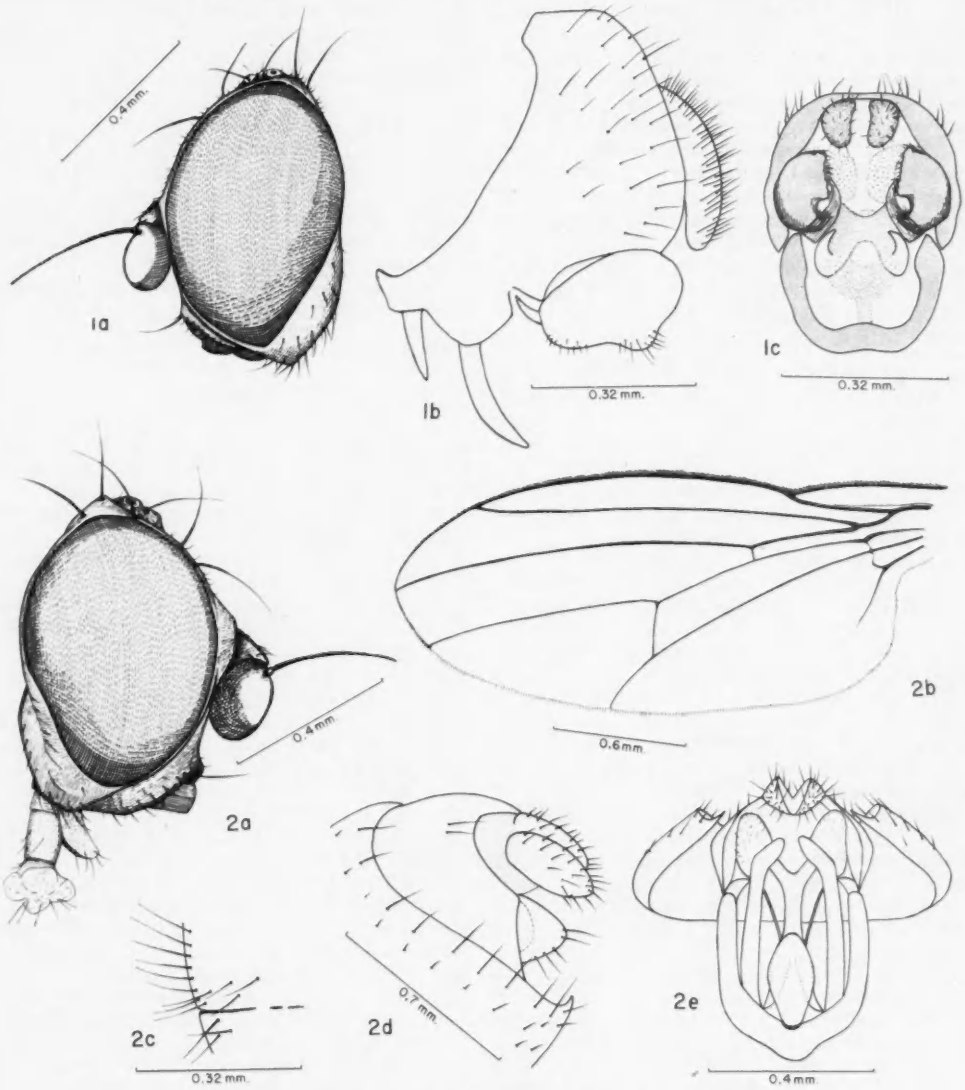

FIG. 1.—*Cacoxenus indagator* Loew. a, Head, lateral view. b, Male genitalia, c, Male genitalia, internal view.

FIG. 2.—*Paracacoxenus guttatus* n. sp. a, Head, lateral view. b, Wing. c, Posteroventral corner of sternopleuron. d, Male genitalia, lateral view. e, Male genitalia, internal view.

section of vein M_{1+2} is slightly longer than is shown in his figure, typically appearing to be about 2.5 times longer than the pentultimate section. The costal fringe thins out gradually beyond the apex of vein R_{2+3} and R_{4+5}. The costa extends a short distance beyond the tip of vein R_{4+5} with just a slight indication of a vein around the margin beyond this point; the fourth costal section is about one-third as long as the third. The r-m crossvein (anterior) is situated at the middle of cell 1st M2.

The abdomen is subshining brown, lightly gray pollinose, and more distinctly gray along the apices of the segments. The ninth tergum of the male is comparatively broad as seen in direct lateral view, but it is narrowed on the dorsal median part (best viewed dorsally). The claspers are broad and blunt, about one-half higher than long, and as seen in both lateral and ventral views each has a blunt setose development in the middle of the inner margin (fig. 1b). The ninth sternum is rather ornate with a strong spur-like process developed on each side; the parameres are large and hook-like (fig. 1c).

Length: Body and wings, 3.2–4 mm.

Paracacoxenus Hardy, new genus

The species from the United States reported by Wheeler (1952) appears to fit the characteristics of the genus *Cacoxenus* in most details. It differs, however, in many respects from typical *Cacoxenus*, based upon *indagator* Loew, and on the basis of the comparison of just the two species it appears to represent a distinct genus.

In the description of *Paracacoxenus* and the comparisons with *Cacoxenus indagator*, it should be noted that some of the characteristics given may be specific and may not be of generic importance. The male genitalia are very strikingly different in the two as is shown in figures 1c and 2e, and also as brought out in the descriptions which follow. *Paracacoxenus* may be characterized by the following details: Male claspers rather small and broadly cone-shaped with a few conspicuous setae at the apices. Ninth tergum rather broad on the dorsal portion and attenuated ventrally; sixth tergum terminating in a strong spine at each posterior corner (fig. 2d). Mesonotum spotted, with a small brown spot at the base of each seta. Inner postalars and presuturals poorly developed, scarcely differentiated from the surrounding setae. Each sternopleuron with a comb-like row of about 10 long hairs extending from the ventral margin to about the middle over the hind portion of the sclerite, the ventral bristle not differentiated from these hairs (fig. 2c). Dorsal bristles lacking on the middle coxae.

Front of male about as wide as long. Mesonotum rather sparsely setose as compared with typical *Cacoxenus*, with only 8 to 10 rows of acrostichal setae present. Costa apparently extending to the apex of vein M_{1+2} although it is hyaline and rather faint in the fifth costal section (between the apices of veins R_{4+5} and M_{1+2}). The extended mouthparts are scarcely one-third as long as the eye height.

In typical *Cacoxenus*, based upon *indagator* Loew, the male genitalia are quite different in development (fig. 1c); the claspers are large and shaped as in figure 1b, the ninth tergum is narrowed medianly and the sixth tergum does not terminate in a spine at each posterior corner. The mesonotum is densely gray pollinose, not spotted, and is rather densely setose with 15 to 20 rows of acrostichal setae. The postalar and presutural bristles are moderately strong. Each sternopleuron has a moderately strong posteroventral bristle, plus a vertical row of inconspicuous short hairs. Each middle coxa has two strong posterodorsal bristles. The male front is one-half longer than wide. The costa ends at or slightly beyond the tip of vein R_{4+5}. The extended mouth parts are about equal to two-thirds the height of the head.

Type of the genus: *Paracacoxenus guttatus* Hardy and Wheeler, new species.

Paracacoxenus guttatus Hardy and Wheeler, new species
(Figs. 2a-e)

Differing from all known related flies by the generic characters given above; however, some of these characters are probably specific for *guttatus* and may not be of generic value.

MALE. *Head:* About one-half higher than long; eyes oval in shape; upper half of occiput very narrow, the back part of the head distinctly concave; lower portion of occiput about equal in width to the gena (fig. 2a). Front rather broad, almost as wide as long, densely brownish gray pollinose; proclinate orbital bristles situated just slightly below the middle of the front, the anterior reclinates situated about two-fifths the distance between the proclinates and the posterior reclinates. Face, genae and clypeus brownish yellow in ground color, densely gray pollinose; a thin black line extending along the lower margin of each gena onto the lower portion of each facial depression; face slightly carinate down the median portion. Palpi and mouthparts yellow, tinged lightly with brown around the apices; each palpus with several black setae around the apex but without distinct bristles. Mouthparts short, the portion extended beyond the oral margin equal to less than one-third the head height (fig. 2a). One strong bristle and about six black setae present in each vibrissal row. Antennae brown, tinged lightly with yellow, the second segment with one moderately stout dorsal bristle, the third segment rounded, just slightly longer than wide. Arista densely pubescent, just slightly over two times longer than the third antennal segment.

Thorax: Densely gray pollinose, with indis-

tinct longitudinal streaks of brown extending down the mesonotum, and with a small brown spot at the base of each seta on the mesonotum; disc of scutellum brownish gray, gray around the margins. Three faint vittae extending longitudinally across each pleuron, one at upper edge of each mesopleuron, one through median portion of each mesopleuron, and one across upper portion of each sternopleuron. Anterior sternopleural bristle equal in size to the posterior bristle; posteroventral portion of the sternopleuron as in figure 2c. Two pairs of dorsocentral bristles present, both situated on the posterior fourth of the mesonotum, the anterior bristles short, about half as long as the posterior ones and situated distinctly behind a line drawn between the posterior supraalars. Inner postalar bristles small and poorly developed, equal in size to the setae of the mesonotum; a pair of strong prescutellar acrostichals present, equal to or greater in size than the anterior dorsocentrals. Only one humeral bristle present, about three-fourths as long as the anterior notopleural bristle; presutural bristle very small, scarcely differentiated from the surrounding setae. Halteres yellow, faintly tinged with brown around the apices.

Legs: Yellow, tinged lightly with brown, the segments moderately slender and without ornamentation; hind basitarsus about two-fifths as long as the tibia, and slightly longer than the combined lengths of the next two tarsal segments.

Wings: Hyaline; third costal section 2.8 times longer than the fourth; last section of vein M_{1+2} about 2.18 times longer than the penultimate section. Crossvein r-m situated at the middle of cell 1st M2. Apical section of vein M_{3+4} just slightly longer than the m crossvein. Costal fringe thinning out rather gradually so that the termination of the fringe is not distinct, extending at least one-third the distance between the apices of veins R_{2+3} and R_{4+5}. The costal vein appears to extend to the apex of vein M_{1+2}, although that portion in the fifth costal section is hyaline (fig. 2b).

Abdomen: Opaque brown, gray at apices of segments. The genitalia are very elaborate and the homologies of the parts are not clearly understood. The general details have been discussed above under the generic characters. The ninth sternum is divided on each side into a pair of elongate slender lobes, the median pair being capitate at their apices. The aedeagus is Y-shaped at its apex and a rather complicated, heavily sclerotized structure fits dorsad to and around the sides of the aedeagus, terminating in a strong black ventral point on each side and having a long slender, almost bristle-like lobe extending posteriorly down each side of the aedeagus. The other details are as shown in figures 2d and 2e and as mentioned above under the generic discussion.

Length: Body and wings, 3.0–3.2 mm.

Female unknown.

Collection records: 4, Dungeness Fork Forest Camp, Olympic National Forest near Sequim, Washington; 17, Glacier View Forest Camp, Wenatchee National Forest near Wenatchee, Washington; 3, Tyee Springs Forest Camp, Pinchot National Forest near Carson, Washington; 1, Polally Forest Camp, Mt. Hood National Forest south of the city of Hood River, Oregon. All specimens were males, collected by the junior author in August, 1951.

Holotype male and three paratypes from Olympic National Forest near Sequim, Washington; thirteen paratypes from near Wenatchee, Washington. Type and six paratypes deposited in the U. S. National Museum. The remainder of the paratypes are in the following collections: Drosophila Type and Reference Collection, The University of Texas; British Museum (Natural History); and the University of Hawaii.

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PACIFIC BRANCH MEETING

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DAVENPORT HOTEL, SPOKANE, WASHINGTION

CHOLINESTERASE AND ALI-ESTERASE ACTIVITY IN ORGANOPHOSPHORUS-SUSCEPTIBLE AND -RESISTANT HOUSE FLIES[1]

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ABSTRACT

Cholinesterase and aliphatic esterase activity were measured colorimetrically in organophosphorus-susceptible and -resistant strains of house flies (*Musca domestica* L.), with acetylcholine and methyl-*n*-butyrate as substrates. The effects of time and enzyme concentration on the hydrolysis of the substrates were determined. The specificity of head and body breis in hydrolyzing both substrates was measured, and distinct differences were shown in levels of esterase activity between the two body regions. Levels of cholinesterase activity were found to be nearly identical in susceptible and resistant flies, but aliphatic esterase activity was much lower in two resistant strains than in the susceptible colony, indicating a possible relationship between this esterase and resistance. Ali-esterase was four times as susceptible as cholinesterase to inhibition by parathion and five times as susceptible to inhibition by para-oxon. With malathion, cholinesterase was twice as susceptible to inhibition as ali-esterase.

Various esterases have been implicated in the toxic action of organophosphorus insecticides to insects (Casida 1955; Hopf 1952, 1954; Lord and Potter 1951, 1954; Metcalf and March 1949, Metcalf et al. 1956). Much is known about the mechanisms of inhibition of the cholinesterases, both in vivo and in vitro, and there is little doubt that the inhibition of acetylcholinesterase by organophosphorus compounds is closely associated with their insecticidal action (Winteringham and Lewis 1959).

However, the importance of cholinesterase (ChE) inhibition as the sole lesion in insect poisoning has been challenged. According to Winteringham and Lewis (1959), other effects, such as the stimulated oxygen consumption, liberation of toxins other than acetylcholine (Ach), the temporary or ineffective nature of pyridine-2-aldoxime methiodide and atropine in reversing the action of anticholinesterases, are not readily explainable in terms of acetylcholinesterase inhibition.

Van Asperen (1958) demonstrated the presence of an aliphatic esterase (Ali-E) in the thorax of house flies, which was distinct from the ChE found in the heads. Although the Ali-E was inhibited in vitro by DDVP at the same concentration as ChE, in vivo studies showed the thoracic Ali-E to be inhibited faster and to a greater degree than ChE.

In studies on the metabolism of organophosphorus compounds in mammals, the authors utilized the colorimetric method of Hestrin (1949) as modified by Robbins et al. (1958) in measuring ChE depression and recovery. It was determined that methyl-*n*-butyrate (Meb), the substrate used by Van Asperen in measuring Ali-E activity, gave a color reaction with hydroxylamine and ferric chloride similar to that given by Ach. Tests were therefore initiated to compare the activity, specificity, and susceptibility to inhibition by phosphates of Ali-E and ChE activity in organophosphorus-susceptible and -resistant strains of house flies.

MATERIALS AND METHODS

Insects.—Three-day-old female house flies (*Musca domestica* L.) were used in all experiments. The susceptible flies were from the regular colony maintained in our laboratory. The resistant strains, the Grothe and Tropical P colonies, were obtained from the Orlando, Fla., Laboratory. Their resistance to malathion and parathion was about 100 and 18 times, respectively (Wilson *et al.* 1959). The Grothe colony has also been shown to be about 4 times resistant to parathion (LaBrecque et al. 1957) and the Tropical P colony at least 20 times resistant to malathion (LaBrecque *et al.* 1958). The resistant strains were maintained in the laboratory without further exposure to insecticide during the experiments.

Insecticides.—Technical-grade parathion and malathion were purified by overnight incubation in pH 8 phosphate buffer to remove impurities (Metcalf 1959). Para-oxon was purified by dissolving in chloroform and extracting several times with 10% sodium carbonate in water. Acetone solutions of all insecticides were prepared prior to use.

Preparation of breis.—Flies were decapitated while under carbon dioxide anesthesia and the heads and bodies stored in the deep freeze at −10° C. All analyses were performed within 24 hours of the time of decapitation. Breis were prepared immediately before analysis by homogenizing in refrigerated phosphate buffer (pH 7.2) with a Potter-Elvehjem glass homogenizer. The homogenates were filtered through glass wool plugs, and the particulate residue was rinsed with additional phosphate buffer. Final concentrations of one head and two bodies per milliliter were used. All samples were kept on ice until assayed.

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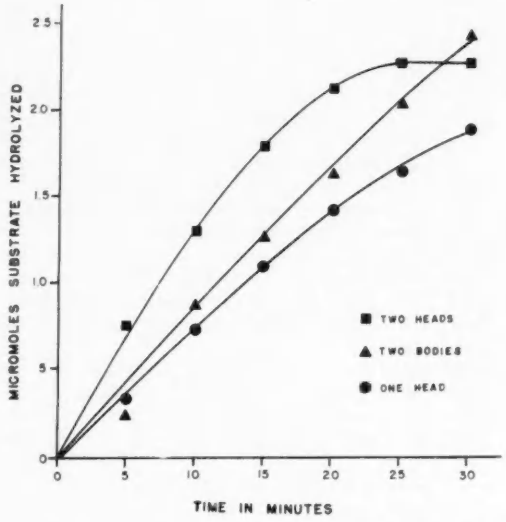


FIG. 1.—Fly head ChE activity and fly body Ali-E activity as functions of time of reaction with substrate using 1 ml. of 2.5×10^{-3} M Ach and 1 ml. of 4×10^{-2} M Meb, respectively.

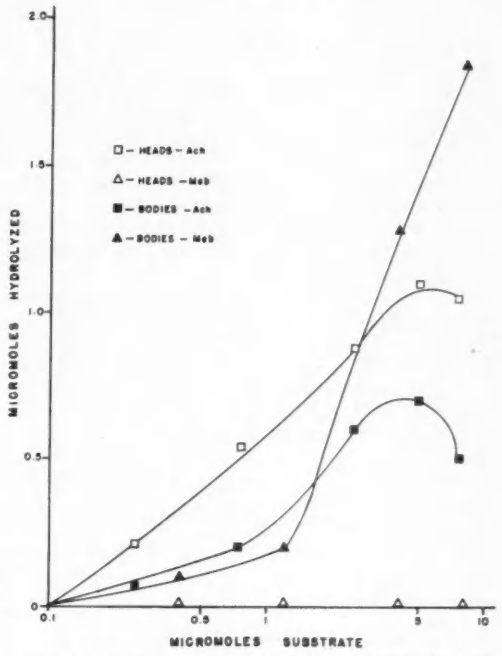
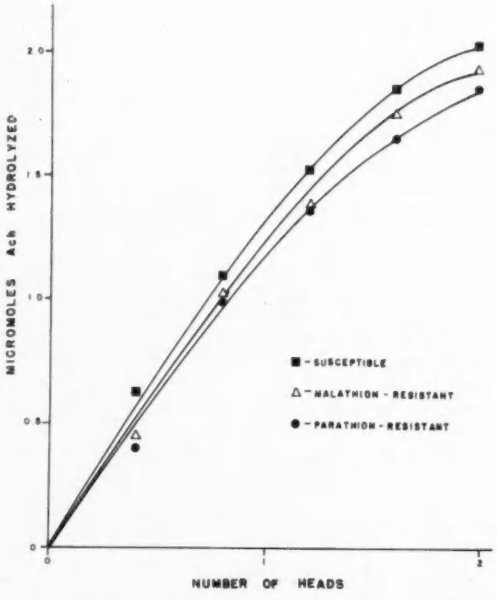


FIG. 2.—Substrate specificity of head and body breis of 3-day-old female house flies with Ach and Meb.



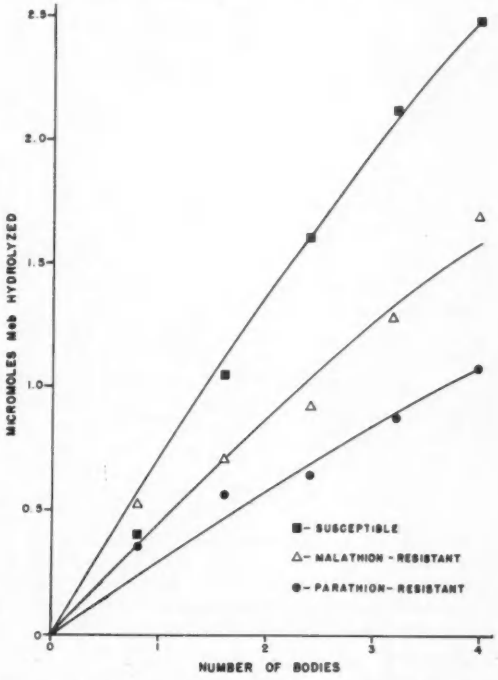


Fig. 3.—Comparison of ChE activity of head breis and Ali-E activity of body breis of organophosphorus-susceptible, malathion-resistant, and parathion-resistant female house flies.

Reagents.—The reagents used for colorimetric assay were the same as those described by Robbins et al. (1958) except that 1 ml. of acetylcholine bromide at 2.5×10^{-3} M and 1 ml. of Meb at 4×10^{-3} M were used as substrates. The hydroxylamine, sodium hydroxide, hydrochloric acid, and ferric chloride reagents were used at the same molar concentrations, but the amount of each was halved. All homogenates were incubated with the substrates for 15 minutes at 37° C. unless otherwise specified, and all colorimetric determinations were based on a minimum of 4 replications for each sample. Owing to the instability of Meb, this substrate was made daily in distilled water at a concentration of 4×10^{-2} M and then diluted 1:10 in phosphate buffer immediately prior to use.

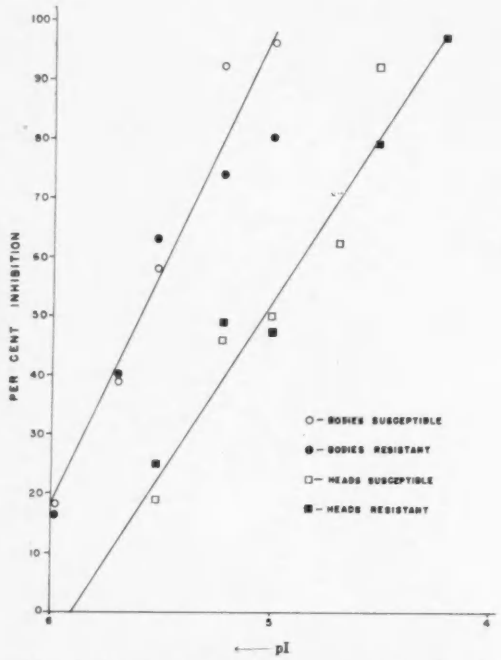


FIG. 4.—In vitro inhibition of head ChE and body Ali-E of organophosphorus-susceptible and parathion-resistant house flies by parathion. pI = concentration of inhibitor.

EXPERIMENTAL

Preparation of standard curves.—Standard curves were prepared for different amounts of 2.5×10^{-3} M concentrations of Ach and Meb. The substrates were incubated in phosphate buffer for 15 minutes prior to the addition of hydroxylamine. Optical densities were determined using a Beckman DU spectrophotometer at 540 mμ. with a 1-cm. light path, and the values were plotted against the micromoles of substrate present in each sample. Linear relationships were obtained for both substrates at the concentrations used.

Measuring effect of time of incubation on hydrolysis of Ach and Meb.—Head and body breis of the susceptible flies were incubated with 2.5μ moles of Ach and 4μ moles of Meb for various periods. At the end of the period the reaction was stopped by the addition of hydroxylamine and the remaining substrate determined colorimetrically. The results (fig. 1) indicate that a linear relationship occurred which extended beyond the 15-minute period regularly used for incubation, when the Ali-E activity of two bodies and the ChE of one head were used as enzyme sources. When two heads were used as the source of ChE a linear relationship was not obtained.

Substrate specificity of head and body breis.—Breis containing one head or two bodies of the susceptible flies were incubated with different amounts of each substrate to determine the effect of its concentration on the rate of hydrolysis. The results are given in figure 2. With Ach the expected inhibition by excess substrate was shown. Inhibition of Ali-E activity by excess substrate did not occur. There was no hydrolysis of the Meb substrate by fly head breis at the concentrations used. This lack of cross-hydrolysis is important in that it enabled the authors to measure the two enzymes separately even though

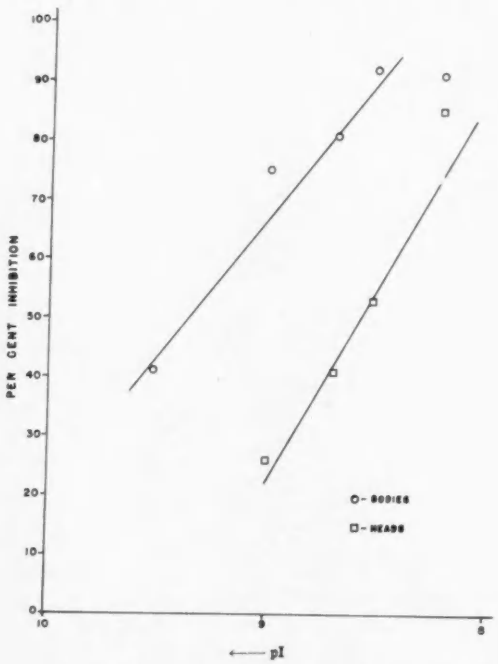


FIG. 5.—In vitro inhibition of head ChE and body Ali-E of organophosphorus-susceptible house flies by para-oxon.

a certain amount of ChE activity is present in fly bodies.

Levels of ChE and Ali-E activity.—Levels of ChE and Ali-E activity in head and body breis of the susceptible and resistant strains were determined by incubating different amounts of breis with standard amounts of each substrate for 15 minutes. The results are given in figure 3. There were no significant differences between levels of ChE activity in any of the strains of flies. Ali-E activity was much lower in the two resistant strains.

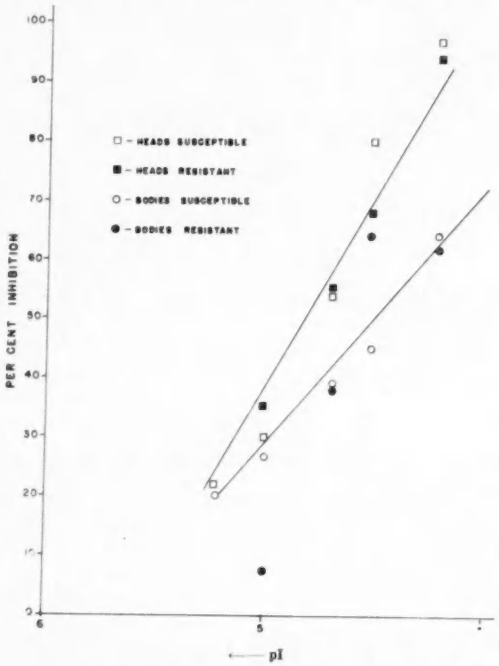


FIG. 6.—In vitro inhibition of head ChE and body Ali-E of organophosphorus-susceptible and parathion-resistant house flies by malathion.

This phenomenon of lower Ali-E activity in resistant flies was unexpected. Ali-E activity was 40% of that of the susceptible flies in the Tropical P (parathion-resistant) colony, and about 60% of that of those in the Grothe (malathion-resistant) colony. Lower Ali-E activity in organophosphorus-resistant flies was recently reported by Van Asperen and Oppenoorth (1959). The present work was done before the authors learned of their findings and serves to substantiate their results.

In vitro ChE and Ali-E inhibition.—The in vitro anti-ChE and anti-Ali-E activity of parathion and malathion were determined colorimetrically for the susceptible and Tropical P colonies of flies. Identical determinations were made with para-oxon on susceptible flies only.

One-tenth ml. aliquots of acetone solutions of the insecticides at appropriate molar concentrations were pipetted into test tubes and the solvent evaporated with a gentle stream of air. One ml. of head or body brei (containing one head or two bodies) and 1 ml. of distilled water were incubated with the insecticide for 15 minutes, and then 1 ml. of substrate was added and the mixture incubated for an additional 15 minutes.

The percent inhibition of both enzymes by increasing concentrations of insecticide is shown in figures 4, 5, and 6. There was little evidence of any qualitative difference between the two esterases in either strain of fly; that is, the same esterase in both colonies was inhibited by a similar amount of insecticide. However, the two esterases were not similar in susceptibility to the insecticides used. With parathion Ali-E activity was four times as susceptible to inhibition as ChE (I_{50} 2.5×10^{-6} vs. 1×10^{-5}). With para-oxon, Ali-E activity was five times as susceptible as ChE ($I_{50}\times10^{-10}$ vs. 2.5×10^{-9}). With malathion, ChE activity was twice as susceptible to inhibition as Ali-E (I_{50} 1.5×10^{-5} vs. 3×10^{-5}).

DISCUSSION

The colorimetric method of assay used in this study has several advantages. It affords a rapid and accurate means of measuring esterase activity. The authors have performed more than 100 analyses a day by this method and have obtained good reproducibility of results. It measures unhydrolyzed substrate and, since the final measurement is of a hydroxamic acid-ferric ion complex, it is of value in measuring the activity of esterases other than those hydrolyzing Ach and Meb.

The decrease in Ali-E activity in the organophosphorus-resistant strains of flies is probably the most interesting information presented here. As discussed by Van Asperen and Oppenoorth (1959), one would expect an increase in Ali-E activity in resistant strains or else a decrease in susceptibility to inhibition by insecticides. Neither of these was found; nevertheless, there appears to be a relationship between lower Ali-E activity and resistance. It is known that measurements of ChE activity in resistant and susceptible strains have consistently failed to show any correlation with resistance (Brown 1958).

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NEW NORTH AMERICAN TABANIDAE. XI. SUPPLEMENTAL NOTES PERTINENT TO A CATALOG OF NEARCTIC SPECIES[1]

CORNELIUS B. PHILIP

ABSTRACT

Apatolestes comastes **fulvipes** (California) and *Tabanus lineola* **hinellus** (Louisiana), each described from holotype female and a male, are new varieties; the latter ranges west to Texas. New synonymy: *Tabanus nigripes* Wied. (= *T. winthemi* Kröb., which is not Neotropical), and *T. vittiger* subsp. *guatemalanus* Hine (which occurs in southern Florida, = *T. v. caymanicus* Fairchild, = *T. bellardii* Szilady). New status: *Atylotus* **tingaureus** (*A. incisuralis* subsp. *tingaureus* (Philip)). The previously unknown male of *Apatolestes albipilosus* Brennan is described, and comments are given on location of types of certain Nearctic species, and on other reportedly Nearctic species that are still unrecognized.

The following information was accumulated too late to be included in the previous paper (Philip 1959, Part X) on the same subject, for which this furnishes a supplement.

Thanks are due Drs. Paul Arnaud, Jr., and H. H. Keifer, of the California Department of Agriculture, for additional specimens of *Apatolestes* and *Atylotus* discussed below. Other acknowledgments are supplied in Part X. Dr. Pechuman has called my attention to a typographical error there, crediting *T. superjumentarius* to Man., which could be changed to Mass.

Apatolestes villosulus (Bigot)

(For references see previous Part X)

Refinement of the concept of this species leaves unassigned the form keyed (Philip 1954) as *A. villosulus* (Bigot) ♂, though intergradation prevents more than varietal separation from *A. comastes*.

Apatolestes comastes fulvipes, new variety

Distinguished in both sexes from the typical form by the unicolorous, bright tawny legs, more definite isolated clouds on cross veins and fork, and usually but not always larger bodies.

Holotype ♀, 12 mm. In all but the above respects, agrees with the typical form including black subshiny front with wide, inflated basal callosity. The entire flagellum is black, and costal cell brown as in var. *willistoni* Brennan which is smaller, has the usual blackish femora and more conspicuous scattering black hairs on the palpi.

Allotype ♂, 12 mm. Also differs from the allotype male of typical form (Philip 1954) in the above respects.

Both, plus a paratype ♀, from Red Bluff,

[1]From the U.S. Department of Health, Education, and Welfare, Public Health Service, National Institutes of Health, National Institute of Allergy and Infectious Diseases, Rocky Mountain Laboratory, Hamilton, Montana.

Accepted for publication October 19, 1959.

Tehama Co., California, 12.vi.1931. In the California Academy of Sciences (CAS).

Paratype males.—1, Potwisha, Sequoia National Park, Calif., 16.vii.1931, E. C. Van Dyke (CAS); 1, Putah Cyn, Yolo Co., Calif., 4.vi.1936, R. M. Bohart; 1, Yosemite Fork, Madera Co., Calif., 8.vi.1940, B. Brookman, T. Aitken, M. Cazier (coll. CBP).

Paratype females.—1, same data as holotype (CBP); 1, Camp Meeker, Calif., 23.viii.1950, Keifer (CAS); 1, Mormon Bar, Mariposa Co., Calif., 7.vi.1940, B. Brookman, T. Aitken, M. Cazier (CBP, teneral).

The topotypic paratype female agrees closely with holotype but is only 9 mm. A male, Santa Rosa Mt., Riverside Co., and a large female, Willets, Calif., 1600 ft., 30.vi.1956, C. B. Philip, off horse, are examples of specimens which intergrade, with femora which are darker brown than tibiae but not black.

Naming this as a variety rather than subspecies is a reversal of my previous sytematic policy. Since under the new Rules, varieties will have nomenclatural recognition analogous to subspecies, most Nearctic infraspecific tabanid names that were cataloged as subspecies will be again listed as varieties in the new catalog. A few that show geographic segregation, such as *Tabanus vittiger schwardti* Philip, will be retained as subspecies.

Apatolestes albipilosus Brennan

1935, Univ. Kansas Sci. Bull. 22: 371, type ♀, Lemon Cove, Calif.; Univ. Kansas.

A female from Corvallis, Oregon, is in good agreement with the type, but is less worn. In addition to the paratype and another from near Fresno, two additional California specimens have been seen from Yosemite Valley, plus the previously unknown male.

Allotype ♂, 14 mm. In good agreement with the female except for the usual sex differences, and readily associated by the distinctive yellow to brown body and appendages, dilute brown fumose wings broadly accentuated on the outer wing margin, moderately narrowed cell R_5, red scutellum and four dark notal lines. Eyes bare, facets sharply enlarged in upper two-thirds. Upper cheeks with considerable black hair grading to whitish below. Apical palpal segments chunky, as long as in female, blunt but not truncated apically, with terminal patches of shaggy black hair. Flagellums, unfortunately, missing.

Modesto, Calif., 27.vii.1958. R. P. Allen. In coll. CBP through courtesy of Dr. Arnaud.

Stenotabanus guttatulus (Townsend)

(For references see Part X)

Since establishment of the lectotype in Part X, the syntype series in University of Kansas has been studied on loan through courtesy of Dr. George W. Byers. The lectotype is intact, labelled "Las Cruces N.M., 6.26;" frontal index 1:3.4, antennae red with black style, and half a dozen obscure black hairs on palp. Length 9.5 mm. Others in the type series are also small, 10 mm. and under, and the styles are black. In contrast, 10 females from southern Utah, Nevada, and California are larger, 11–12 mm., and have red to brown styles; the palpi may be entirely white-haired or with a few scattering black ones.

The syntypes of *S. cribellum* have wider fronts (1:3.3) than the type of syn. *S. currani*, but it is obvious that more specimens from Mexico are needed to decide if the differences from the true *S. guttatulus* stated previously by me will hold.

NEARCTIC HORSE FLIES WITH HOOKED ANTENNAE

The prolongation of the dorsobasal tooth of the antennal plate into a hook or thumb has apparently developed independently in Tabaninae in several parts of the world but is most elaborated in the Neotropics where members of both diachlorine and tabanine flies have developed this character. It is evident, however, that it cannot be given equal taxonomic weight in the various groups in which it has appeared (e.g., the Nearctic *T. imitans* Walk. and var. *excessus* Stone). There are two related, closely-knit tabanine elements in the southeastern Nearctic fauna which are isolated geographically from relatives in the Neotropics. Both groups have sparsely hairy eyes. This, however, is another polyphyletic character.

Agkistrocerus Philip

1941, Canadian Ent. 73: 6, 13; 1942, Proc. New England Zool. Club 21: 57.

The two species, *megerlei* (Wied.) and *finitima* (Stone), are most closely related to Neotropical species variously assigned to *Dicladocera* and *Dasychela*. The confused nomenclatural status of these flies has been discussed by Fairchild (1958), who considers the *guttipennis* and *unicolor* groups as warranting at least subgeneric distinction. *Agkistrocerus* was initially proposed, also as a subgenus of *Dicladocera*, but will be treated as a genus in the catalog pending clarification of the Neotropical relationships. While large, fleshy labella, relatively wide fronts, and hairs on subepaulets and sides of subcalli relate the above species to Fairchild's *guttipennis* group, they diverge in quadrate callosities touching eye margins, banded eyes, black-lined abdomens, and wings with isolated clouds.

Hamatabanus Philip

1941, Canadian Ent. 73: 6, 13; 1942, Proc. New England Zool. Club 21: 57; 1952, Florida Ent. 35: 152.

The three species, *carolinensis* (Macq.), *annularis* (Hine), and *sexfasciatus* (Stone), form a compact group with no near Neotropical relatives, though the sparsely hairy eyes, clear wings and patterned abdomens relate to certain Nearctic *Tabanus* without the peculairly hooked antennae.

Other nearctic *Tabanus*, e.g., *atratus* Fabr., and *americanus* Fors., have antennal plates with exaggerated teeth of different structure which do not warrant special attention though Palaearctic and Neotropical relatives have been separated in superfluous genera, *Styporrhamphis* and *Astigmatophthalmus*.

Atylotus thoracicus (Hine)

Tabanus thoracicus Hine 1900, Canadian Ent. 32: 248.

A male from Coleman, Mono Co., Calif., 5.vii. 1958, W. E. Simonds, extends the range nearly to the Pacific Coast. The specimen is typical except for a predominance of black hairs on the dorsum of abdomen, and some on palpi and in postocular fringe.

Atylotus tingaureus (Philip), new status

Tabanus incisuralis subsp. *tingaureus* Philip 1936, Canadian Ent. 68: 159, type ♀, Libby, Mont.; coll. CBP.

A somewhat similar appearing, pallid male of *A. incisuralis* (Walker), taken at same time and place as *A. thoracicus* above, is quickly differentiated by the sharply black flagellar style and lack of tall, postorbital bristles. Males of all Nearctic *Atylotus* spp. studied, except *A. incisuralis*, have this row of yellow, black, or mixed upright bristles across the vertex, unless worn. Both males and females taken together of "subsp." *tingaureus* Philip at Eagel River, SE Alaska, 11.vii.1952, by W. C. Frohne, and a pair from Douglas, Alaska, show such rows of black bristles, which now indicates that the latter is specifically distinct. Only remnants remain on the worn type and paratype but these bristles are also found on other females from California, Oregon, Washington, British Columbia, and Montana, though they are longer in the males.

The Eagle River male may be described as allotype (coll. CBP).

More robust than most *incisuralis* males, 13 mm. Vestiture predominantly golden-yellow with sparse black hairs intermixed on parafacials, palpi, sides of notum and abdomen. Hairs on eyes dense yellow. Hairs of postorbital row and on scape black, twice as long as ocular hairs. Antennae entirely orange-red. Body and femora entirely blackish with indefinite brown shadows on sides of tergites 2 and 3.

In *incisuralis* males, the vestiture is predominantly whitish, at least the style is darkened, and the postorbital bristles do not protrude above the pile of the eyes. Femora are often extensively reddish apically and costal cells more nearly hyaline. While the smaller homotype male of *A. duplex* (see Part X) is also dark and has a similar, black postorbital fringe, the vestiture of face, pleura, and first two sternites is whitish, while female *A. duplex* are very different without frontal callosities.

Hybomitra sexfasciata (Hine)

(For references and synonymy see Part X)

This is one of the Holarctic species discussed by Lindroth (1957), who concurs in the synonymy given in Part X. However, *H. lapponica* (Loew) is incorrectly also given Holarctic status on the basis of mistaken synonymy with the Nearctic *H. astuta* (Osten Sacken) and questioned with *H. typha* (Whitney). Both of these are distinct species, having wider fronts and callosities in specimens that I have compared, and more plainly patterned thoraxes and abdomens, while the latter also has reddish antealar tubercles. The relationship, however, is evident.

Tabanus nigripes Wiedemann

1821, Dipt. Exot. 1: 75.

Tabanus winthemi Kröber 1931, Konowia 10: 295.

Comparison in 1953 of a female of *T. nigripes* from Georgia with two cotypes of *T. winthemi* Kröber in Vienna Museum labelled "S. America, Coll. Winthem" also reveals close agreement as well as an error in the locality.

Tabanus lineola hinellus, new variety

Tabanus "quinquemaculatus Wied.," Hine 1904, U.S. Dept. Agric. Bull. 44: 58; "1903" (issued May 1904), Second Rept. Gulf Biol. Sta. Bull. No. 2: 83 (lapsus).

Tabanus quinquevittatus, Hine "1903", ibid. p. 68; 1906, Ohio Nat. 7: 26; 1907, Louisiana Bull. No. 93: 55. Not Wiedemann 1821, Dipt. Exot. 1: 84 (see Philip 1942, Psyche 49: 38).

Tabanus lineola var.? Philip 1942, Psyche 49: 34.

Though Hine did not include this species in his 1903 catalog, he described and figured both sexes shortly thereafter as specifically distinct from *lineola* on average larger size, "decidedly more yellowish, and the upper purple band of the eye is noticeably narrower." While the wide fronts of the females and even yellow and brown abdominal stripes give specimens a more distinctive appearance from typical *lineola* than used for differentiation of some of the Neotropical members of the group, intergradation in all characters in accumulating material has discouraged continued recognition since Hine first set this apart. Whether this variation is intra- or interspecific and can be settled without rearing is questionable. Insular variation among Antillean *lineola* was discussed (Philip 1957) and var. *cubanus* Szil. was recognized on the basis of red scutellums, dark femora, and narrow fronts in the females.

Separation of the present variety, found chiefly in coastal Mississippi, Louisiana, and Texas, still leaves an unsatisfactorily variable residue in *lineola*, but it at least narrows attempts to refine the systematics of this Nearctic complex. It is named for the late Professor J. S. Hine who first recognized the form and generously sent me a pair from his early Louisiana studies along with other representative species.

Holotype ♀, 14 mm. Eyes (relaxed) with the usual *lineola* pattern but not as heavy as in the typical form; outer margins typically extended. Front buff-gray-pollinose, moderately convergent below, and subparallel in the upper third, a few black hairs at vertex; index 1:4.5, callosity dark

brown, pear-shaped, narrowly separated from eye margins, grading into a short median, blackish extension above. Subcallus buff-pollinose. Face and cheeks whitish-pollinose and pilose. Antennae orange red, the apical annulus brown; sparse black hairs on the two basal segments and dorsal angle of the third; plate short and wide, about one-fourth longer than wide, the style subequal in length. Palpi pale yellow, predominantly white-haired with a few black ones; swollen basally, attenuated, about two-thirds longer than thick.

Thorax dorsally and scutellum blackish, covered with gray bloom and sparse yellow and black hairs, imperceptibly lined between the wing bases; antealar tubercles reddish. Pleura gray with white pile. Coxae and bases of the femora dark gray with pale yellow hairs, the fore and hind pairs of femora broadly reddish at the knees, and on the apical third of the mid pair. Tibiae reddish with pale yellow hairs, a few black ones intermixed in the hind tibial fringe, apical half of fore pair and their tarsi black. Wings glass-clear including costal cell, veins yellow, no spur veins.

Abdomen with three yellow and two subequal, even, black-haired brown lines, and black-haired discontinuous patches on sides of first four tergites, the last two tergites black except for pale hairs mesally. Venter entirely reddish with yellow hairs, the last two sternites darker, and a terminal patch of upright black hairs.

Cameron, La. Aug. 14–28, 1903. J. S. Hine (det. as "quinquevittatus Wied.").

Allotype ♂, 12.5 mm. Except for usual sexual differences closely resembles the holotype, though abdominal lines are less prominent because worn. Head wider than thorax, subhemispherical, the enlarged facets occupying three-fourths of the total eye area, pale reddish; lower area of small black facets continued up hind margin to vertex as a wide band. Apical palpal segment subovoid, hardly twice longer than thick with a blunt, downward-pointed, apical nipple.

Same data as holotype.

Paratypes.—LOUISIANA: 2♀, same data as holotype (one in coll. L. L. Pechuman); ♂, ♀ Delta Wildlife Refuge, Plaquemines Parish, 24.vii.1940, E. S. Hathaway; 2♂, Fenton, 6.v.1948, Evans and Flint (coll. L.L.P.); ♀, Slidel, 25.vi.1948, Beamer. MISSISSIPPI: ♀, Biloxi, 20.viii.1948; 4♂, 3♀, Waveland, 9.vii.1934, R. H. Beamer (pair in Univ. Kansas). TEXAS: ♂, Hidalgo, 24.vi.1948, S. S. Roback (night); ♂, Brownsville, x.1942, E. S. Ross; ♂, same, 11.ii.1950, T. F. Biemler (coll. L.L.P.); ♀, same, 16.ix.1942, T. M. Burns; 3♀, Galveston, May, F. H. Snow (one in Univ. Kansas); ♀, Ft. Crockett, 8.ix.1943, George Berg; ♂, 3♀, Beach, 17 mi. W. Sabine Pass, 10–12.vi.1956, H. E. Evans and E. G. Mathews (coll. L.L.P.); ♀, Southmost, Cameron Co., 13.iv.1950 Michener, Rozens, Beamers, Stephens; ♂, Hidalgo, 24.vi.1948, S. S. Roback (night).

These agree with respective types. Frontal indexes of females vary between 1:4.0 to 1:4.7.

Separation of this form still leaves an unsatisfactory and probably composite residue assigned to typical *lineola*, with fronts of females varying from 1:4.6 to 1:7.2, the latter a Walker, La., specimen with darker, uneven stripes. A considerable series from southern Florida and a few from Louisiana were excluded because of darker, more uneven abdominal stripes and more whitish median stripes, or males with markedly fewer, larger eye facets. Perhaps rearing will demonstrate these intermediate forms not to be separable from var. *hinellus*. A dark race in Michigan with narrow, pale median lines is analogous to Neotropical var. *plangens* Wied., but wings are not tinted. The reliability of the reduced eye pattern of *hinellus* observed by Hine in fresh specimens cannot be assessed with the material at hand. However, several relaxed specimens show narrower bands than usual including the Southmost, Texas, paratype (front 1:4, length 15 mm.). A small (12 mm.) typical *lineola* female taken at the same time as the last has heavier eye pattern, uneven stripes, the median one whitish, and front 1:4.5.

Tabanus vittiger subsp. **guatemalanus** Hine

1906, Ohio Nat. 7: 24. Fairchild 1942, Ann. Ent. Soc. Amer. 35: 180.

Tabanus bellardii Szilady 1926, Biol. Hungarica 1(7): 23. Pechuman 1957, Ent. News 68: 118. NEW SYNONYMY.

Tabanus truquii, Bequaert 1940, Rev. Ent. 11: 352 (partim). Not Bellardi 1859, Saggio Ditter. Messic. 1: 64. Not Stone 1938, U.S. Dept. Agric. Misc. Publ. 305: 123.

Tabanus vittiger subsp. *caymanicus* Fairchild 1942, Ann. Ent. Soc. Amer. 35: 180. Philip 1957, Amer. Mus. No. 1858: 6. NEW SYNONYMY.

Tabanus lineola subsp. *scutellaris*, Philip 1949, Amer. Midland Nat. 43: 436 (Florida record). Not Walker 1850, Ins. Saund. Dipt. 1: 27.

This species is established in the Nearctic Region in southern Florida, as reported by both Pechuman and Philip for synonyms (op. cit.). Though Bequaert (op. cit.) was mistaken in assigning this form to *T. truquii* and was too inclusive in distribution (his Texas records were undoubtedly based on *T. colombensis* Macquart, syn. *T. amplifrons* Kröber), he was correct in considering Central American specimens as inseparable from the Antillean material. It is even quite possible that this form will also be inseparable from typical *T. vittiger* Thomson 1868, when males eventually become available from Galapagos Islands.

Because of moderate variation in the color pattern of females, in part due to wear, the head characters of both sexes provide the most reliable diagnostic characters. Two Galapagos *T. vittiger* females have unusually wide fronts (indexes, 1:3.5) and antennal plates a little more excised,

but a third without antennae has index of only 1:4.2; callosities yellow to cherry-red. Frontal indexes of females from southern Mexico, British Honduras, Guatemala, Cayman Is., Bahamas, and Puerto Rico, otherwise inseparable, vary from 1:4 (including two Cayman types of *caymanicus* and a Campeche, Mexico, specimen) to 1:4.4 for two specimens from Bahama Is. and Dist. Fed., Mexico. Indexes of two paratypes of *guatemalanus* and the Honduras specimen are 1:4.2 and have yellower callosities than usual, but so does the Grand Cayman paratype of *caymanicus*. Separate maintenance of the insular and continental forms, including available males, does not appear justified.

Through courtesy of Drs. P. J. Darlington and J. Bequaert of Museum of Comparative Zoology, the unlabelled types of subsp. *caymanicus* Fairchild were studied. Of two females and one male (without abdomen) from Cayman Is. series, the best preserved of the former and the latter have been labelled holotype and allotype respectively in accordance with Fairchild's statement. The other female, and his Cuba female have been labelled paratypes. The front and palpi of the type are as figured by Bequaert (op. cit.) for *T. truquii* but the antennal plate is not as excised. Contrary to Fairchild's key characters, the types are not more black and white than is seen in other reddish-brown, insular and continental specimens. The topoparatype is a little smaller and has a pale brown rather than cherry-red callosity with more pronounced median extension than in the holotype. The palpi of the broken allotype are not as produced apically as in some males from other localities, but there is moderate variation in this respect. The extent and hairiness of the enlarged facets is the same.

The dates on types published by Fairchild are for the Oxford University Expedition. Actual dates on respective separate labels are as follows: holotype, 2.vi.1938, Little Cayman light trap; allotype, 29.v.1938, same; paratype, 16.vi.1938, Grand Cayman, S. Coast of S. Sound.

Diachlorus badius Kröber

1928, Archiv f. Schiffs- u. Tropenkrankheiten 32: 50 "Georgia, Coll. Winthem," in Vienna Nat. Hist. Mus.

The type compared by me in 1953 differs from a Georgia *D. ferrugatus* (Fabricius) female in several respects, including wider front, larger callosity, shining blackish face, pleura, and fore femora, and longer antennae. Though I could not identify it with any other South American species, where the genus has shown a considerable burst of speciation, I decided, pending confirmation, to remove the name from the Nearctic catalog on the following grounds: The locality cannot be definitely assigned to United States, and most of Winthem's specimens came from Latin America, as did the two Brazil types of the strictly Neotropical species, *Stibasoma fulvohirtum* Wiedemann, of which Kröber (1932) records another type of Berlin "von Georgia," also possibly a Winthem specimen. Of some two dozen species of *Diachlorus*, only *D. ferrugatus* has vigorously invaded the Nearctic fauna in the Southeast and Atlantic Coast, reaching Costa Rica to the south; only two others, *D. curvipes* (Fabricius) and *D. jobbinsi* Fairchild, are known as far north as Panama. Kröber's Brazil record for *D. ferrugatus* is very doubtful.

OTHER UNRECOGNIZABLE SPECIES

Of other tabnines listed by Stone (1938) as unrecognizable, the types of the two below in BMNH, also from Georgia, were restudied in 1958. Neither could be associated with the familiar pattern of that area and continued assignment, even questionably, to the Nearctic fauna without confirmation over a long period, of specimens additional to the unique types appears unwarranted. One, *T. leucomelas* Walker, was redescribed by Philip (1941) on notes supplied by Mr. Oldroyd. The other, *T. tetropsis* Bigot, is a male with exceptionally wide, flat head, and the grayish, trivittate abdominal pattern plus the pronounced spur veins at base of R_5 relate to such eastern Mediterranean species as *T. albifascies* Loew. No Georgia species are even close to either. In view of these facts and the unreliability of many of Bigot's locality labels, I have little hesitation in omitting both names from the forthcoming catalog.

T. pubescens Macquart from America has previously been dropped by me though Fairchild (1956) states the poorly preserved type "is not certainly Neotropical." The narrow front and other characters bear out Kröber's (see Philip 1941) tentative relation to *Chelommia* more than to any Nearctic species. It will still be omitted from the Nearctic catalog. In any event, the identity is not of importance since the name is preoccupied by Strøm.

This leaves a residue of unrecognizable, but apparently bona fide Nearctic species, not discussed in Part X, identities of which may never be clarified because of loss or confusion of types; several are preoccupied in any event. These include: *Chrysops provocans* Walker (uncertain syn. of *carbonarius* Walker since wings of type are missing), *T. cingulatus* Macquart (preoccupied), *T. ferrugineus* Palisot de Beauvois (preoccupied), *T. nebulosus* Palisot de Beauvois (preoccupied), *Therioplectes frenchii* Marten, and *Therioplectes sussurus* Martin (both equal *Hybomitra*). It is to be hoped that studies in progress by J. A. McAlpine of the Canadian Department of Agriculture on the *H. frontalis/septentrionalis* complex will elucidate the now unrecognizable *Tylostypia labradorensis* Enderlein (type in Berlin Museum).

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THE ULTRASTRUCTURE OF THE HEART OF THE COCKROACH, BLATTELLA GERMANICA[1]

GEORGE A. EDWARDS[2] AND CYRIL E. CHALLICE[3]

ABSTRACT

The dorsal vessel, associated nerves, ganglia, and diaphragm were examined in thin sections by the electron microscope. The muscle fibers of the dorsal vessel have tonic characteristics, except for more numerous mitochondria and more fully developed endoplasmic reticulum. Striking continuities of the endomembranes occur, particularly between endoplasmic reticulum and plasma membrane, membranes of mitochondria and reticulum, and internuclear membranes. The muscle cells abut longitudinally by simple plasma membrane apposition, transversely by cell border modifications similar to the classical intercalated discs. The axons of the ventral ganglia are suspended in either simple mesaxons, or in mesaxonal tunics. A given axon may contain endoplasmic reticulum, synaptic vesicles, membrane-limited (and non-membrane-limited) neurosecretory granules, or combinations of these components. The significance of the morphologic arrangements is discussed in relation to neuronal and muscular transmission. The cells of the diaphragm resemble actively secreting hypodermal cells. The secretion bodies are closely associated with the Golgi complex, the latter apparently providing a mechanism for active transport from the cytoplasm to the cell exterior.

The fine structural details of cardiac muscle (Moore and Ruska 1957), conducting system (Muir, 1957b; Caesar et al. 1958), and neuronal relations (Couteaux and Laurent 1957; Fawcett and Selby 1958) of the vertebrate heart have been investigated by electron microscopy. The vertebrate heart is cellular, the individual fibers being separated from each other by modified regions of apposing plasma membranes, the intercalated discs. The latter are but special forms of the ubiquitous desmosome. Thus, it is logical to expect that the insect heart also should be cellular, and the cells interrelated by some mechanism such as a disc or modification thereof. The present study was undertaken to resolve this question and also to elucidate the fine structure of the insect heart-muscle fiber, the associated diaphragm, ganglia, and nerves. The results have shown that the insect heart-muscle cell has a micromorphology more typical of insect tonic muscle than of the vertebrate cardiac muscle. However, the intercellular apposition is mediated by cell-border modifications resembling those of the classical intercalated disc of the vertebrate.

MATERIAL AND METHODS

An adult cockroach, *Blattella germanica* (L.), was opened along the midventral line so as to expose the dorsal vessel along its entire length. A 2 percent solution of osmium tetroxide in veronal-acetate buffer at pH 7.4 was introduced, immersing the vessel, which was then dissected out, cut into lengths of 2 to 3 mm., and further fixed in vials in fresh osmium tetroxide for 1 hour. The material was subsequently washed in buffer, dehydrated in a series of graded ethanols, infiltrated with a solution of butyl and methyl methacrylates in the proportion of 9:1, further infiltrated and embedded in a similar solution of methacrylates catalyzed with 1.5 percent Lucidol, and polymerized at 46° C. for 36 hours. Sections of 30mμ thickness were cut with a Fernández-

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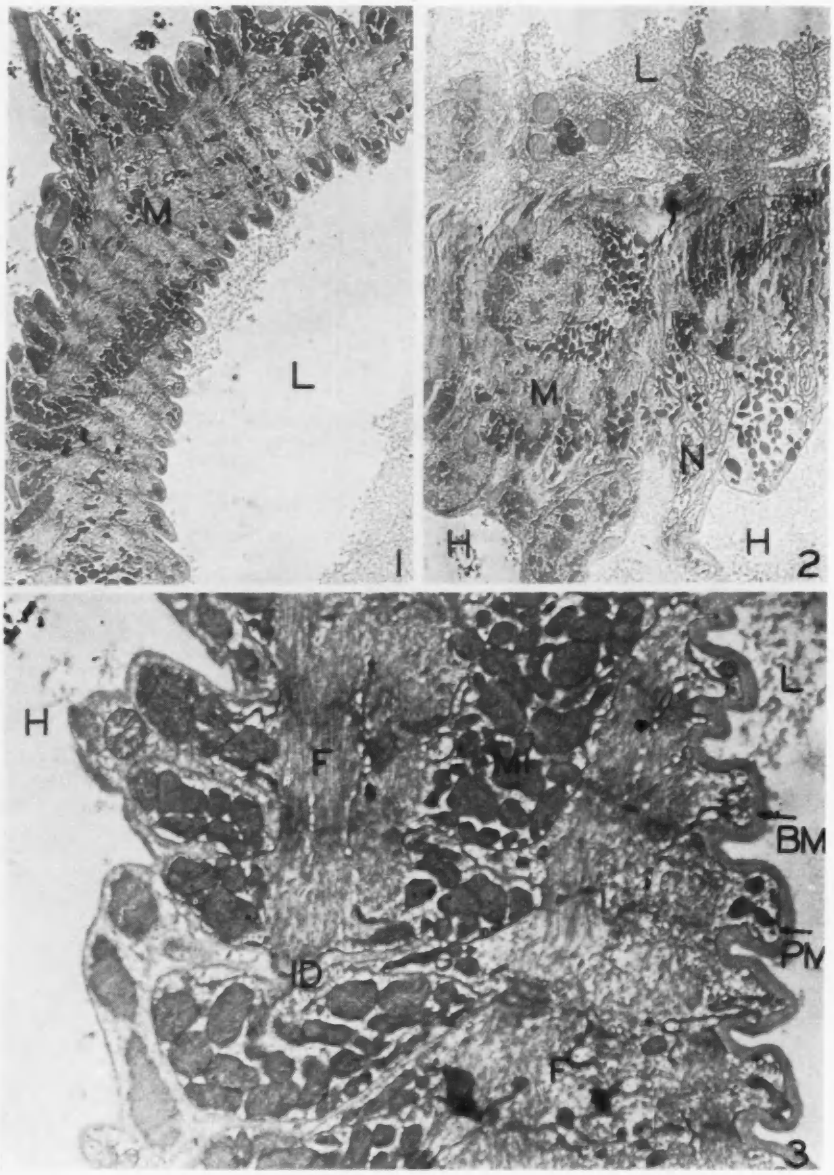


FIG. 1.—Approximate cross-section through two cells of the wall of the dorsal vessel, showing general distribution of muscle-fiber constituents and fiber outline (M = vessel, L = lumen). x4,000.

FIG. 2.—General view, cross-section, of part of the wall of the dorsal vessel, showing relation of nerve (N) to muscle fiber (M). The nuclei visible at the lower left belong to cells of the diaphragm, bordering upon the haemocoele (H). Above, in the lumen (L) of the vessel, several haemocytes may be seen. x4,000.

FIG. 3.—Detail of junction of the two cells shown in fig. 1. Transversely, the cells are separated by an intercalated disc (ID); longitudinally, by plasma membrane apposition only (arrows). The folds of the fiber are smaller on the luminal side (L) than on the haemocoelomic side (H). The mitochondrial aggregates may be seen in the folds (at left) and between filament (F) bundles (center). Covering the muscle fiber at the left may be seen the basement membrane and little cytoplasm of a diaphragm cell. x15,000.

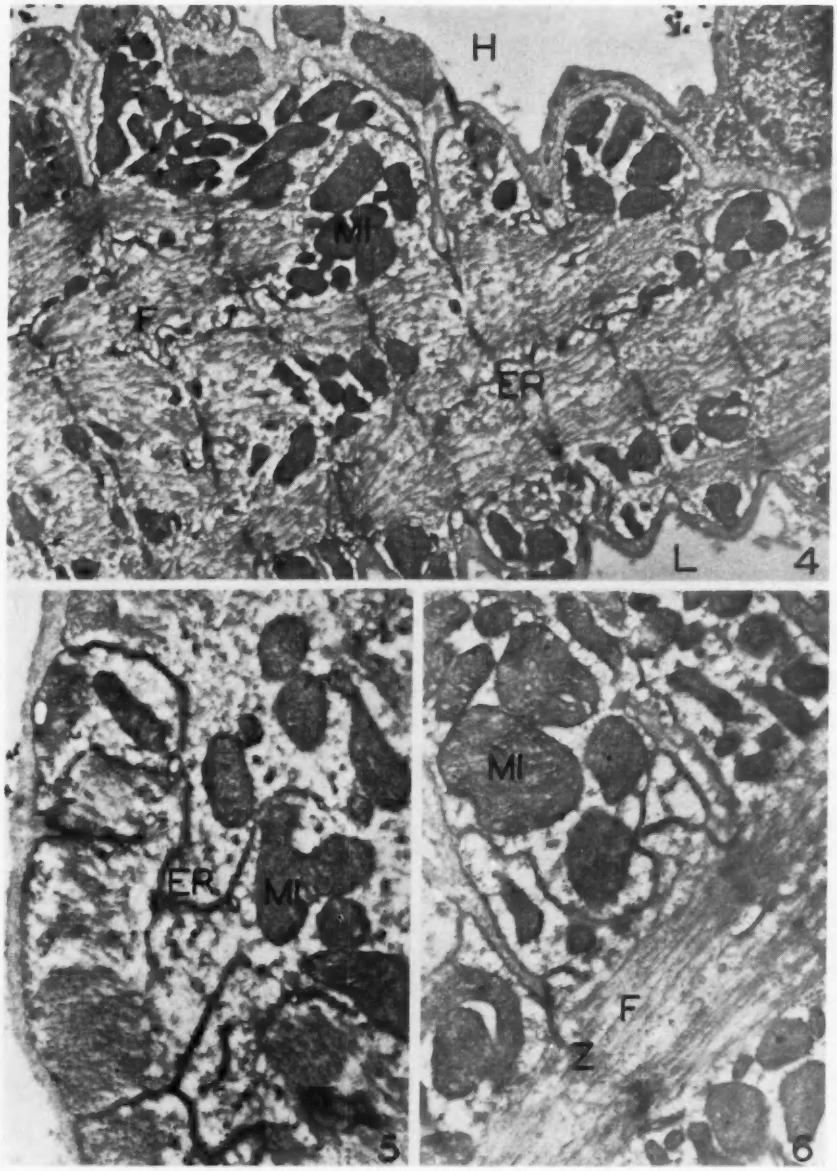


FIG. 4.—Detail of dorsal vessel, showing separation of myofilament bundles (F) by mitochondria and endoplasmic reticulum (ER). The filaments possess only the Z cross-striation. Overlying the fiber on the haemocoelomic side (H) may be seen a nucleus, little cytoplasm, and basement-membrane material of a diaphragm cell. x15,000.

FIG. 5.—Detail of the periphery of a muscle cell, showing continuity of deep invaginations of the plasma membrane with vesicles and tubules of the endoplasmic reticulum (ER). Some of the mitochondria (MI) connect with each other and with membranes of the reticulum. x30,000.

FIG. 6.—Detail of invagination of the plasma membrane at Z-band level. At the base of the invagination (arrow) the membrane is thickened and continuous with vesicles of the reticulum, in turn continuous with Z-band vesicles of the myofilaments (F). The mitochondria (MI) show connections with each other, with reticulum, and with plasma membrane. x30,000.

Morán diamond knife on a Porter-Blum microtome. The sections were mounted on formvar films lightly stabilized with carbon, and observed in a Siemens' Elmiskop I.

RESULTS

A. *Muscle.*—The heart, or dorsal vessel, consists of a hollow cylinder, the muscular wall of which is one cell thick (figs. 1–4, 8). The muscle fibers are circularly arranged. The cell borders are highly rugose so that the wall in cross section presents an accordion-like appearance (fig. 1), the folds on the luminal side being deeper and more convoluted than those on the haemocoelomic side.

The lumen of the vessel often showed coagulated plasma and haemocytes (fig. 2); however, these will not be considered in the present report.

In many respects the relations of the contractile material, itochondria, and endoplasmic reticulum were similar to those in the tonic muscle fibers of the gut (Edwards et al. 1956). Nevertheless, the fibers are sufficiently different to warrant a complete description.

The muscle fiber is surrounded by a filamentous basement membrane (figs. 3–8) averaging 130 mμ in thickness. The filaments of the membrane are arranged in a nonorderly felt-work. The cell per se is limited by a plasma membrane, which at intervals is deeply invaginated, and by way of such invaginations continuous, either directly or indirectly, with the membranes of the endoplasmic reticulum (figs. 3–11). The connection is usually at the level of the Z band of the myofilaments, i.e., the reticulum and the Z band together form a distinct "grundmembran." The mitochondria are numerous, large, irregular, and form aggregates in subplasmalemmal pockets (figs. 3, 4, 6, 8) as well as in the perinuclear residual cytoplasmic area (figs. 2, 7, 8), and among or around myofilament bundles (figs. 3, 4). Cristae mitochondriales are complete and closely packed upon each other as if layers of corrugated cardboard. The mitochondrial matrix is dense and finely granular. The outer mitochondrial membrane is sometimes continuous with the outer membrane of a nucleus (fig. 7) and with the elements of the endoplasmic reticulum (figs. 5, 6, 11). In the subplasmalemmal region, the mitochondria are often continuous with microindentations of the plasma membrane (fig. 9).

The Golgi complex is small and is located in the residual cytoplasmic area.

The endoplasmic reticulum comprises a continuous system of membrane-limited vesicles, tubules, and saccules from plasma membrane to the nucleus, and is intimately related to the contractile material at the level of the Z band transversely, and between myofilament bundles longitudinally. Little pinocytotic vesiculation of the plasma membrane occurs. Rather, microvesicles are observed only as that part of the endomembrane system in the regions of deep invagination of the plasma membrane (figs. 5, 6, 11). Indeed, invaginations are often so deep, and the vesicles and tubules of the endoplasmic reticulum so closely associated with the plasma membrane, that it is difficult to distinguish cell borders from the reticulum (fig. 11). Frequently what appears in a section to be a bridge between two cells is, after closer scrutiny, seen as a portion of one cell forming a narrow neck between two deep furrows of the plasma membrane or between discontinuous membranes of the endoplasmic reticulum, which in turn are continuous with the plasma membrane (fig. 11).

In the periphery of the cell the plasma membrane at the base of the invagination may be thickened (fig. 6) and continuous with vesicles of the endoplasmic reticulum. These are continuous with the microvesicles of the Z line and with the triads of the endoplasmic reticulum surrounding the myofilaments at the junctions of the isotropic and anisotropic regions.

The myofilaments are generally not arranged into discrete myofibrils but rather exist as irregular bundles or fields of contractile material. Only one type of myofilament is apparent. The myofilaments are divided into sarcomeres delimited by Z bands. The other cross-striations found in mammalian cardiac and skeletal muscle have not been observed in these preparations.

The cells are multinucleate, the nuclei often being aggregated into groups of two or three (fig. 7) within a small area of the cell. The nuclei are preferentially located towards the luminal side of the cell. The nucleus possesses a double-membraned envelope, finely granular matrix, scattered chromatic material and one or more nucleoli (figs. 7, 8). It is significant that the nuclei may be interconnected by means of their outer membranes, i.e., they may possess a common perinuclear cisterna (fig. 7).

Adjacent cells are separated from each other in three ways. In those regions of longitudinal apposition (fig. 3) the cells are separated by their unmodified plasma membranes and an interspace of 10 mμ. Transverse separation may be by wide spacing (figs. 9, 11), the intercellular space occupied by loosely arranged basement-membrane material. Where the separation of the cells directly interrupts the longitudinal myofilament pattern (figs. 3, 9, 10) an intercalated disc is formed, the ultrastructure of which appears to be identical with that of the disc of the vertebrates. In the disc region the apposing cells interdigitate, the convolutions being less complex than those of the classical intercalated disc. The plasma membranes of the disc are specialized in being thickened, vesiculated, and continuous with microfilaments. The latter are continuous with the myofilaments in what would be the isotropic region of the contractile material were it not interrupted at this point. The intercellular space of the disc

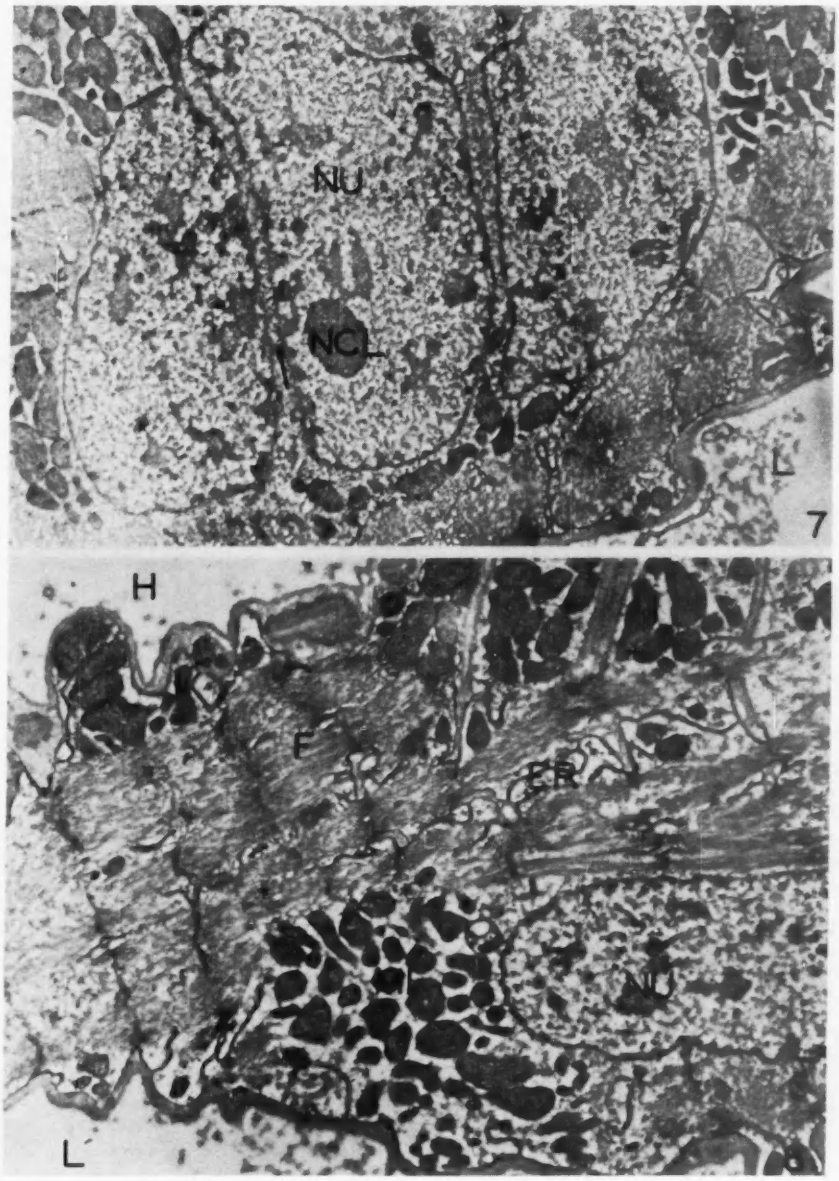


FIG. 7.—Three nuclei, near the luminal side (L) of the muscle fiber. Nucleolus (NCL) prominent. The two nuclei to the left are interconnected by way of their outer membranes (arrow). Some of the perinuclear mitochondria are attached to the outer nuclear membrane. A small Golgi apparatus is seen above the left nucleus. x15,000.

FIG. 8.—Mitochondrial aggregates (MI) in the peripheral folds and in the residual cytoplasmic area at a nuclear (NU) pole. Elements of the endoplasmic reticulum (ER) separate myofilament bundles longitudinally and form vesicular aggregates at Z-band level. x15,000.

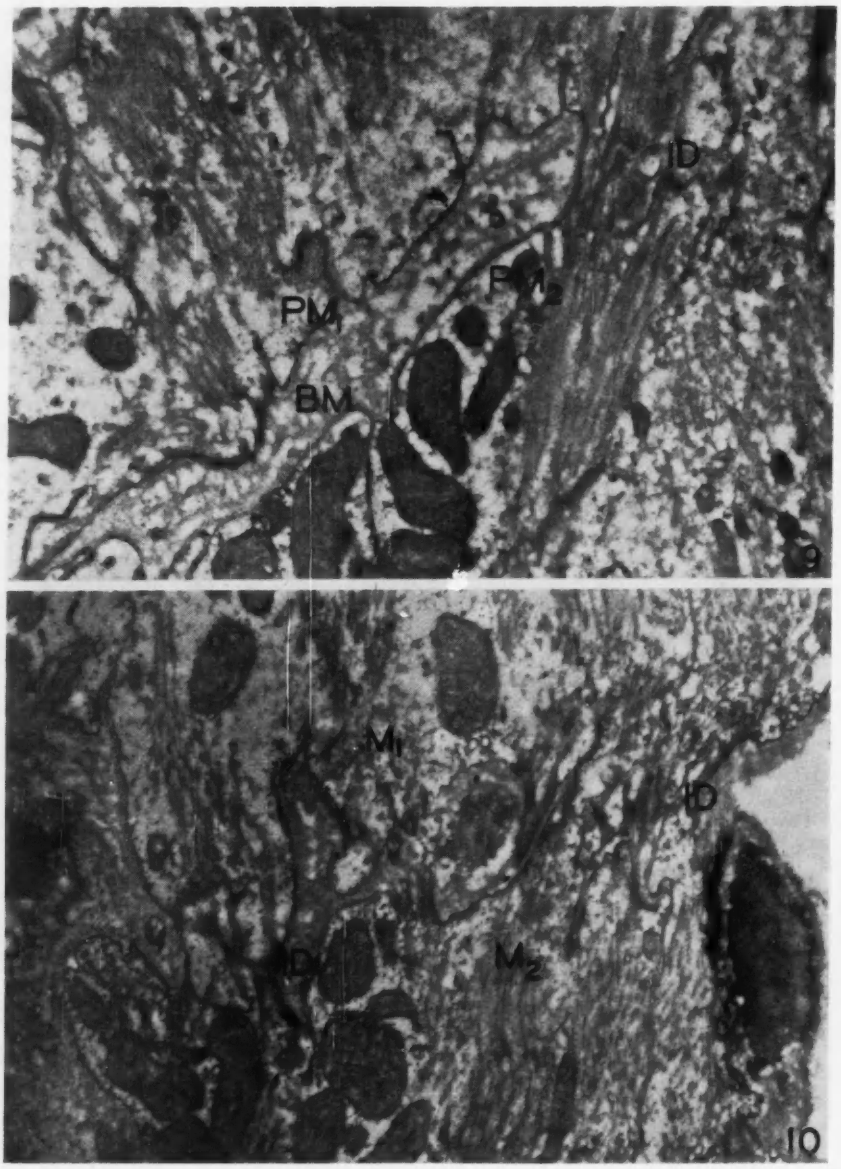


FIG. 9.—Detail of transverse fiber abutment. At the left the plasma membranes (PM1 and PM2) of the two cells are widely separated by basement-membrane material (BM). At region of intimate apposition the plasma membranes and interspace are modified into an intercalated disc (ID). x30,000.

FIG. 10.—Transverse cellular abutment by means of a complex, convoluted, intercalated disc (ID) as well as by basement-membrane material between the two cells (M1 and M2). At the right may be seen an area of densely packed material within the looser filamentous basement membrane. x30,000.

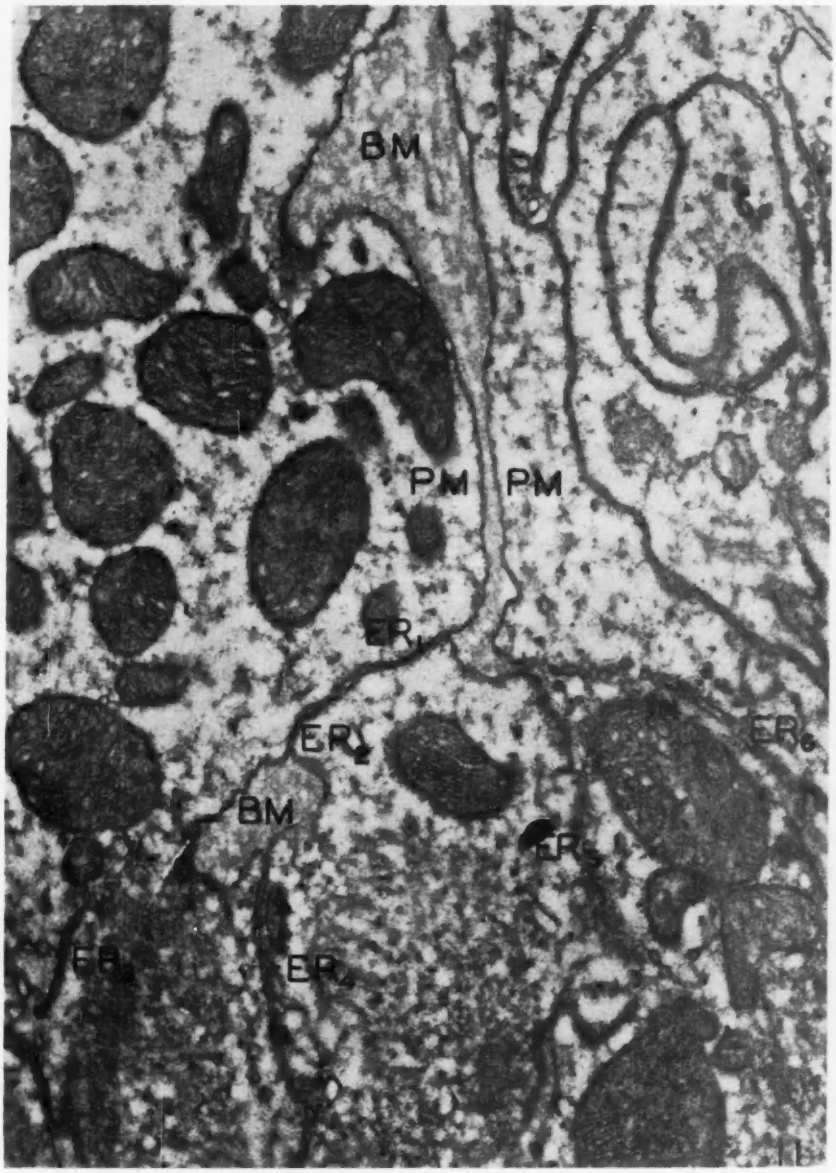


FIG. 11.—Detail of the periphery of a muscle cell. The irregular cell border is indicated by the plasma membrane (PM) and the surrounding basement membrane (BM). Invaginations of the plasma membrane are directly continuous with the endoplasmic reticulum (ER1 and ER2) constricting a portion of the cell. The continuity is maintained by a narrow strip of cytoplasm (arrow) from one part of the cell to another. Elsewhere in the cell sarcomeric regions are distinctly marked out by tubules and vesicles of the endoplasmic reticulum (ER3–ER6) facultatively continuous with small invaginations of the plasma membrane. The mitochondria show the densely packed cristae typical of muscle cells that work continuously, as in the heart, or at high frequency, as in flight muscles. x60,000.

contains a substance of medium electron density, presumably representing the intercellular cement. In mammals the corresponding substance is believed to be a mucoprotein (Rinaldini 1958). This being an insectan heart, the material here could well be arthropodin or a protein-chitin complex.

B. *Nerve.*—The present preparations were favorable for detailed observation of the structure and relations of ganglia (figs. 12–16), nerve (figs. 2, 12), and neuromuscular junctions (figs. 17–19), on the ventral surface of the heart.

The ganglion is ensheathed by the thick, filamentous felt-work of the basement membrane of the lemnoblasts. The axons of the ganglion are surrounded by mesaxons formed by the multiple invaginations of the lemnoblast plasma membrane. The individual axon is suspended within a single turn of the mesaxon, or within several loose mesaxonal turns, forming a "tunicated" axon (cf. Edwards et. al. 1958a). Thus, all the axons are nonmedullated. Axonal type, however, cannot be determined without several thousand serial electron micrographs for reconstruction of interaxonal relations. In the present preparation, as in the ocellus (Edwards and Ruck 1958), it even is difficult to distinguish pre- from postsynaptic axons because a given axon may contain synaptic vesicles, neurosecretory granules, endoplasmic reticulum, and mitochondria, all at a given time or in a given area, or may contain only one axoplasmic organelle in the plane of sectioning. In general, it can be assumed, however, that those axons containing synaptic vesicles are presynaptic. The neurosecretory granules appear to be of at least two types (figs. 12–14, 16). Large, dense, spherical, nonmembrane-limited granules occur in some axons (fig. 13) whilst less dense, irregular, membrane-limited granules may be seen in other axons (fig. 14). These two types have not been observed within a given axon, and it is perhaps of further significance that these neurosecretory granules occur in only the axons of large diameter.

The nerve between the ganglion and the heart muscle (figs. 2 and 12) was seen as a number of parallel, lemnoblast-enclosed axons which fan out on the surface of the heart wall, and terminate in simple neuromuscular junctions.

The neuromuscular junctions (figs. 17–19) observed were similar to those previously observed in the wasp (Edwards et al. 1958a). The synapsing axons contain numerous synaptic vesicles averaging 25 mμ in diameter, a few larger elements of the endoplasmic reticulum (fig. 17), and small mitochondria (figs. 17, 18). The axon is separated from the muscle fiber at the region of most intimate synapsis by the respective plasma membranes and their interspace of 5–10 mμ. In one synapse (fig. 18) the synaptic membranes appear to be discontinuous, suggesting a direct exchange between axon and aposynaptic region of the muscle. The aposynaptic region of the muscle is characterized by mitochondria and numerous granules of uniform density and size, averaging 10 mμ in diameter.

C. *Diaphragm.*—The diaphragm appears in the electron microscope as a sheet of tissue, one cell thick distally and several cells thick proximally where it meets the dorsal vessel (figs. 2, 12, 20). The basement membrane of the latter cells contains modified regions which are markedly denser in the electron micrograph than the rest of the membrane substance (figs. 1, 3, 4, 10, 21, 22) but have a similar type of internal structure. At the region of most intimate contact of diaphragm and vessel, the basement membranes of the diaphragm and muscle cells fuse together (figs. 4, 12), and the thinned-out diaphragm cells overlie the outer surface of the vessel like a tightly fitting glove, even extending into the infoldings of the muscle cells. At the point of junction (figs. 12, 20), irregular, almost amoeboid cells mediate the contact between the diaphragmal sheet and the muscle cylinder. The morphology of the covering cells is similar to that of the cells in the distal sheet.

In their micromorphology (figs. 21, 22), the cells of the diaphragm appear to be similar to hypodermal cells, and in particular to actively secreting hypodermal cells. The cell is bounded by a filamentous basement membrane of variable width surrounding a very irregularly outlined plasma membrane. This may form deep, labyrinthine invaginations (fig. 22), the narrowed openings of which, significantly, show "intracellular" bar formations at their narrowest gaps. Vesiculation of the plasma membrane is common where it forms the lining of the labyrinths. The nucleus of the cell of the diaphragm shows no unusual characteristics. The cytoplasm, however, is filled with few mitochondria but many membranes of the endoplasmic reticulum (fig. 21) and Golgi apparatus (fig. 22). The reticulum is of the rough membrane profile type, i.e., RNP granules are attached to the cytoplasmic side of the membrane. The Golgi apparatus comprises dictyosomal and microvesicular elements, the latter being intimately associated with membrane-limited secretion bodies. These are single membrane-limited bodies of various sizes (fig. 22) up to a micron in diameter, possessing a matrix of medium density. It would appear that some substance is secreted across the membrane of the endoplasmic reticulum and that by increasing accumulation and membrane growth, the secretion body increases in size to a certain limit and then disrupts, the substance apparently being carried to the exterior by way of the Golgi vesicles and the labyrinths. The nature of the material within the secretion bodies is not known at present. It could, however, be the precursor of the basement membrane material.

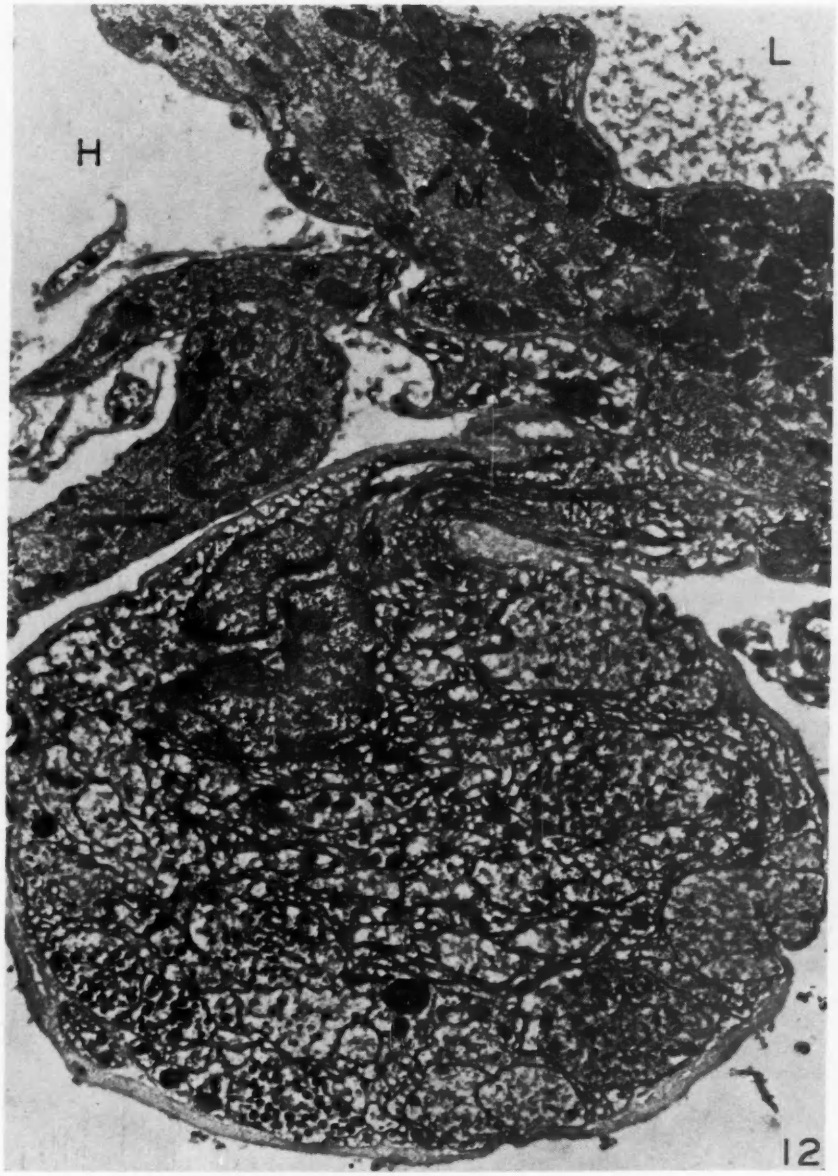


FIG. 12.—Section through a ganglion (G), and nerve (N) extending from it toward the muscular wall (M) of the dorsal vessel. At left is part of the diaphragm (D), which becomes several cells wide at its point of junction with the vessel. x15,000.

DISCUSSION

The arthropods possess only striated muscle, the structure of which varies according to the specialized function. Thus, there has been described from the insect at least three different types of fiber, i.e., tonic, as in the gut; low frequency tetanic, as in leg muscles and lower-insect flight muscle; and high frequency tetanic, as in the flight muscles of higher insects and in the tymbal muscle of the cicada (Edwards et al. 1956;

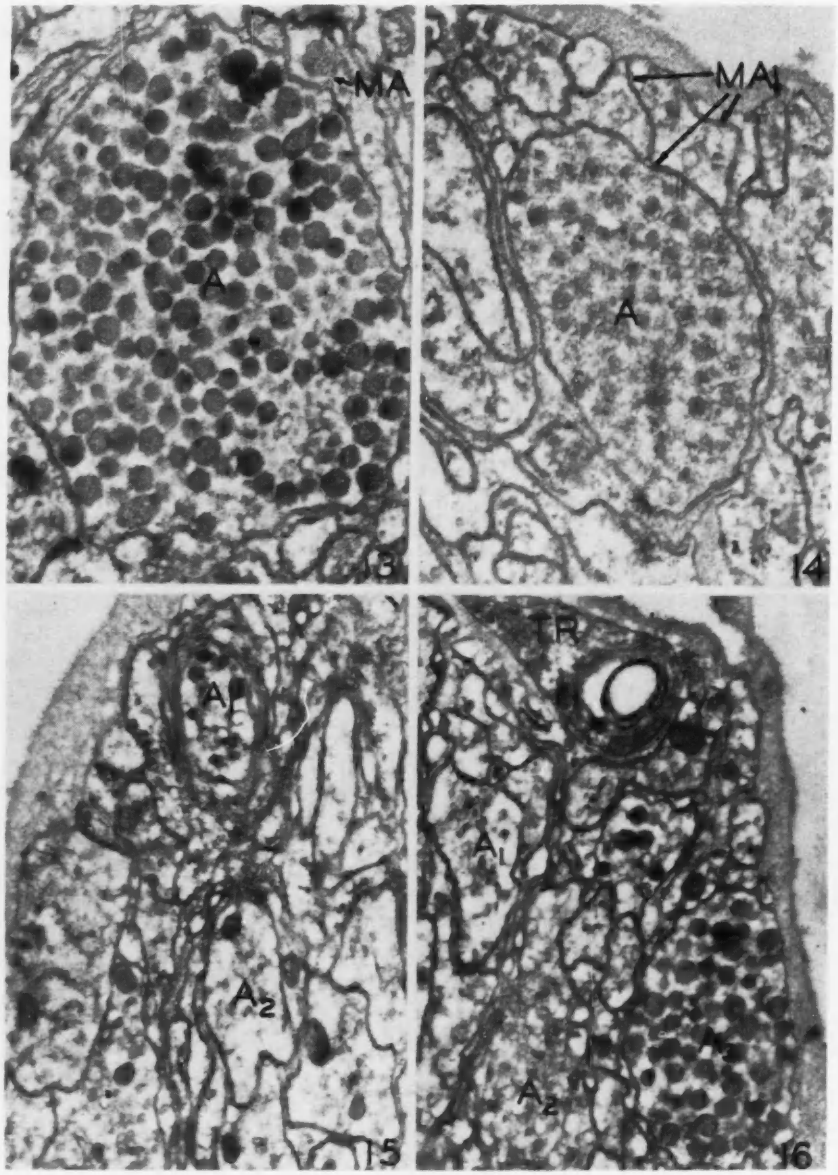


FIG. 13.—Section of large-diametered axon (A) containing dense, nonmembrane-limited neurosecretory granules. The mesaxon (MA) is at upper right. x40,000.

FIG. 14.—Large-diametered axon (A) suspended in a cisterna formed by numerous mesaxons (MA). This axon contains neurosecretory granules of irregular form, little density, and enclosed within membranes derived from the endoplasmic reticulum. x40,000.

FIG. 15.—Periphery of the ganglion, showing the filamentous basement membrane of the sheath cell. The contained axons may be enclosed within a single turn of the mesaxon (A2), or within a number of loose turns (A1). x30,000.

FIG. 16.—Periphery of the ganglion, showing relation of tracheoblast and contained trachea (TR) to the ganglion. Axons may contain vesicles (A1), endoplasmic reticulum and membrane-limited granules (A2), or nonmembrane-limited granules (A3). x30,000.

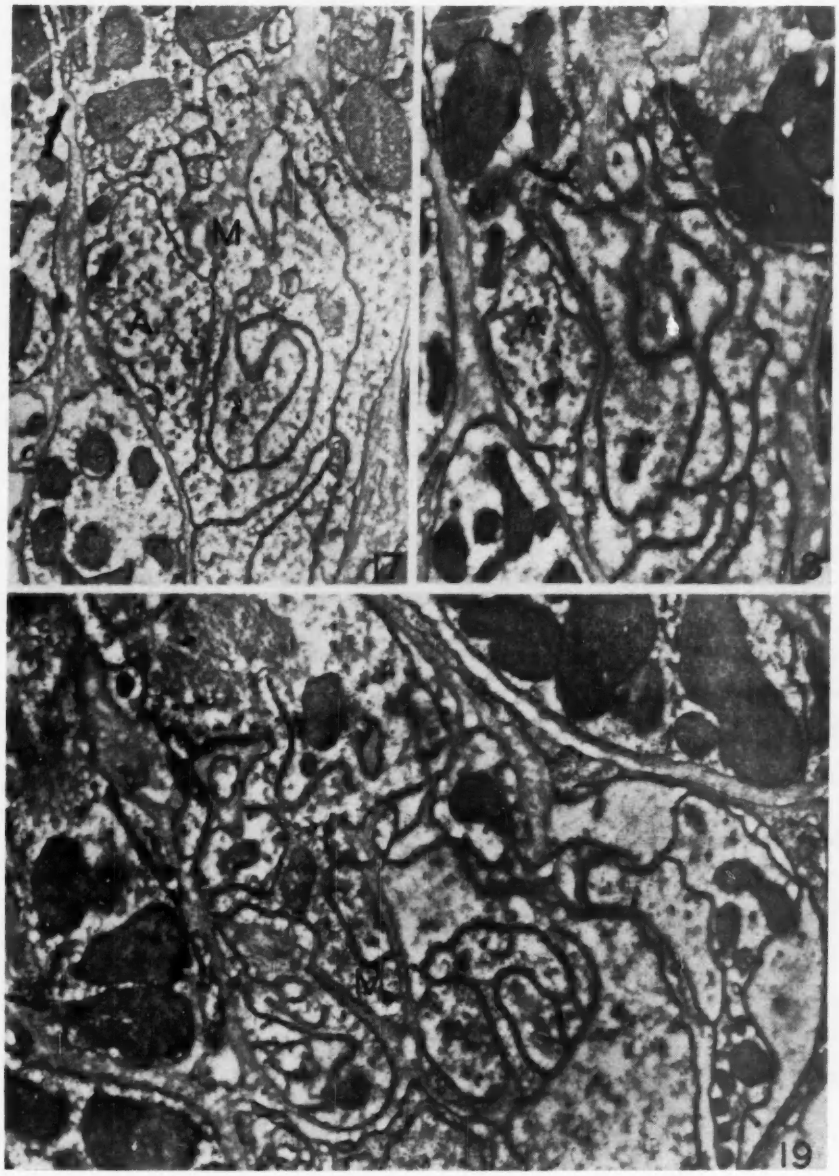


FIG. 17.—Neuromuscular junction in the dorsal vessel (M). The synapsing axon (A) contains a small mitochondrion, numerous synaptic vesicles, and a few larger vesicles of the endoplasmic reticulum. x30,000.

FIG. 18.—Neuromuscular junction in the dorsal vessel. The region of contact between the muscle fiber (M) and the synapsing axon (A) is indistinct, due apparently to discontinuity of the membranes. x30,000.

FIG. 19.—Axon (A) and muscle fiber (M) near the synaptic region. Although separated by basement-membrane material, the two show the characteristics of a synapse, i.e., synaptic vesicles in the axon and aposynaptic granules in the muscle fiber. x30,000.

Edwards et al. 1958a, 1958b). The vertebrate also possesses tonic and tetanic fibers similar in their ultrastructure to those of the insect tonic and low frequency tetanic (Edwards et al. 1956; Edwards, 1958). The vertebrates have, in addition, a cardiac muscle, which in its fine structure has most of the characteristics of tetanic striated muscle, but which evolutionarily has been considered as derived from both smooth and striated muscle. It was thought at the beginning of the present study that clarification of the micromorphology of the insect heart would provide some evidence in the direct line of sequence of heart-muscle fiber phylogeny. The results proved the contrary, the insectan heart muscle having micromorphologic characteristics more closely related to tonic muscle.

Some light has been thrown, however, on the phylogeny of the intercellular relations in the heart, i.e., the modifications of the adjacent plasma membranes resulting in the formation of an intercalated disc. The fine structure of the intercalated disc has been studied in fish (Challice and Edwards 1960), Amphibia (Grimley and Edwards 1958), reptiles (Fawcett and Selby 1958) and mammals (Sjöstrand and Andersson 1953; Sjöstrand et al. 1958; Van Breemen 1953; Poche and Lindner 1955; Muir 1957a, 1957b; Caesar et al 1958; Challice and Edwards 1958). The detailed fine structure of the cockroach intercellular abutment is similar to that of the vertebrate, thus now extending the occurrence of the intercalated disc from the insect up through the mammals. In retrospect it is not too surprising that such a modification of abutting cell borders should occur over such a wide phyletic range, inasmuch as in its fine structure the intercalated disc is similar to, or identical with, the desmosome. The desomosome (synonyms: intercellular bar, intercellular bridge, node of Bizzozero, prickle, knot of Ranvier) is the most common method of intercellular contact and adhesion (cf. Weiss 1958; and Fawcett 1958 for discussion), and has been observed in all phyla from the coelenterates (unpublished data) through the vertebrates. It appears early in embryonic cell development and indeed occurs even in cultured cells when they are permitted to develop into a multilayered tissue.

Of particular significance in the cells of the dorsal vessel is the relationship between plasma membrane and endoplasmic reticulum. The plasma membrane is frequently deeply invaginated, the invaginating membrane being continuous with membranes of the endoplasmic reticulum at the levels of the Z bands of the myofilaments. Invaginations are often so deep and the continuity with reticular membranes so distinct, that in section one gets the impression that small cytoplasmic areas have become isolated. It seems unlikely if the three-dimensional picture were completed, that isolation would have in fact taken place, but this observation, combined with the difficulty in demonstrating conclusively the demarcation between plasma membrane and endoplasmic reticulum, not only gives conclusive evidence on the close relationship between these membranes but suggests that they may be interchangeable. Such a hypothesis would form a basis for a theory of the development of a plasmodium from a group of cells, for example during the ontogeny of a multinucleate, striated muscle cell. The hypothesis would also provide a mechanism for the formation of single cells from a syncytium.

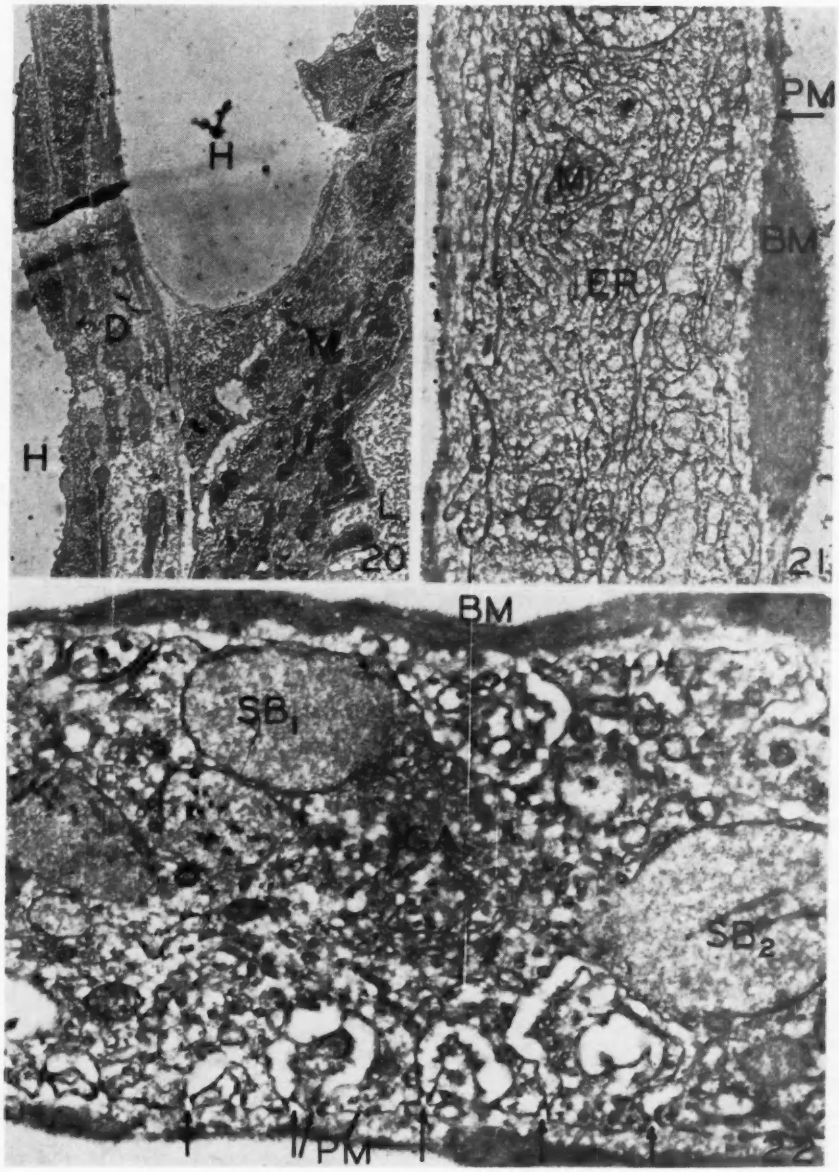
The heart of the cockroach is well innervated by processes from ganglia presumed to be autonomic. Nerve cells have not been detected previously in the wall of the vessel itself (Beard 1953). In the present study, cardiac ganglia, nerves, and neuromuscular junctions were observed and their fine structure was revealed. As previously found in an insect peripheral nerve (Edwards et al. 1958a, 1958b; Edwards 1959) and in the ventral nerve cord of the cockroach (unpublished observations) the axons of both nerve and ganglion associated with the heart are suspended within simple mesaxons, or within a

EXPLANATION OF PLATE IX

FIG. 20.—Low-magnification view of connection of diaphragm (D) with dorsal vessel (M). At the junction, ameoboid cells of the diaphragm spread over the outer surface of the heart; the fused basement membranes of heart and diaphragm forming an effective ion barrier. x7,800.

FIG. 21.—Detail of part of a diaphragm cell, showing small mitochondria (MI), numerous membranes of the endoplasmic reticulum (ER) in the cytoplasm, and basement-membrane material (BM) external to the plasma membrane (PM) of the cell. x30,000.

FIG. 22.—Area of a diaphragm cell with all the morphologic signs of active secretion. In the cytoplasmic center is a complex Golgi apparatus (GA). On either side are secretory bodies (SB_1 and SB_2). The membranes of SB_1 appear continuous with some of the Golgi membranes. The secretory material of SB_2 appears continuous with the cytoplasmic matrix within the Golgi zone. A continuous line of vesicles of the Golgi apparatus extends from the central zone to the borders of the labyrinthine involutions of the plasma membrane. Thus a mechanism of transport of the formed material to the outside by the Golgi vesicles is suggested. Of unusual interest are the "intracellular" bars (arrows) across the openings of the labyrinths. The less dense material between the labyrinthine openings and the basement membrane (BM) suggests that the material being formed is precursory basement-membrane material. x35,000.



loose tunic formed by several mesaxonal turns. Thus, all insectan axons investigated to date are nonmyelinated. Of note, for the interpretation of physiologic events, i.e., the relation between current flow and chemical control, is the finding that a given axon in a ganglion or nerve may contain synaptic vesicles and neurosecretory granules simultaneously, or one or the other. Of further interest is the fact that two types of granules exist, one nonmembrane-limited, the other enclosed within membranes apparently derived from the endoplasmic reticulum. On the basis of the postulated role of the endoplasmic reticulum in intracellular conduction (Ruska et al. 1958; Peachey and Porter 1959), it is tempting to suggest that the spectrum from electrical to

hormonal communication in invertebrate nerve transmission, as visualized by Roeder (1953), is represented micromorphologically by the presence of vesicles, through mixed vesicles and granules and membrane-limited granules, to nonmembrane-limited granules. It is further likely that the vesicular and neurosecretory elements are temporal as well as spatial in their occurrence, i.e., that a given axonal area may at one time contain vesicles and at another time granules.

The junction between nerve and muscle cells in the dorsal vessel is of the simple type of synapse, as previously seen in the leg muscle of the wasp (Edwards et al. 1958a). Again, in the present preparations, evidence of membrane discontinuity in the synaptic region suggests a possible direct transmission of axonal material. An alternate possibility is the reduction of the dimension of the synaptic region to a few millimicrons, i.e., to the level where single molecules of nerve and muscle can interact.

Previous studies of other organisms have shown direct continuity of the plasma membrane with the membranes of the endoplasmic reticulum, mitochondria, and the outer nuclear membrane (McAlear and Edwards 1959). Prime examples of such continuities are seen in the cells of the cockroach dorsal vessel, particularly between plasma membrane and endoplasmic reticulum, endoplasmic reticulum and mitochondria, and between nuclear membranes. Such continuity provides great cytoplasmic mobility for the interaction of linked enzyme systems, and further increases the efficiency of action of the cell through the distribution of functions among specialized systems. It is logical that such a morphologic architecture be available in a cell such as that of the heart, which must function uninterruptedly over a long period of time.

Cytoplasmic changes involving increase in ergastoplasm and mitochondria have been shown in actively secreting hypodermal cells (Wigglesworth 1957). The present study has demonstrated unexpectedly that the cells of the diaphragm also showed all the micromorphologic features of actively secreting cells, not only in ergastoplasm and mitochondria, but also in the form of secretion bodies, extensive Golgi apparatus, and in plasma membrane modification. The nature of the secretion is unknown. From the micrographs it appears to be the precursor of the basement-membrane material. Thus, the secretion would perhaps be similar to that in the formation of mucoprotein by the hypodermal cells during cuticle formation. Of considerable interest, micromorphologically, are the association of the secretion bodies with the Golgi apparatus, and the "intracellular" modifications of the labyrinthine invaginations of the plasma membrane in the diaphragm cells. Secretion has been associated with membranes of the endoplasmic reticulum (Palade 1956) and with the Golgi apparatus (Farquhar and Wellings 1957). In effect, due to continuity of, and interconvertibility of membranes of the endoplasmic reticulum and Golgi apparatus, it is quite likely that the initial stages of secretion involve rough membrane-profiled endoplasmic reticulum, and the secondary stages of removal of the products involve the smooth membranes and Golgi membranes, the latter forming the final "packets" carried to the cell surface. Certainly in the present study the secretion bodies are within the Golgi zone, and the membranes of the two are often continuous. Further, lines of vesicles are seen between Golgi zone and active cell border, suggesting these to be a mechanism for active transport from the cytoplasm to and through the cell border.

An unusual feature of the cell border of the diaphragm cell is the labyrinthine infolding, reminiscent of the border of human amnion cells (Edwards and Fogh 1959), and rat-kidney tubule cells (Ruska, et al. 1957). In the latter two types of cells some basement-membrane material accompanies the invaginated plasma membrane. In the cockroach diaphragm cell the basement membrane does not penetrate the invaginations, but rather modifications of the plasma membranes occur at the entrances to the labyrinths such that essentially "intracellular" bars are formed across the interspace. Physiologically their function can only be guessed at. They could serve as ion barriers, or as passive filters. Architecturally, such modifications are important as examples of extension of intercellular membrane relations to the level of relations between membranes within a given cell.

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BIOLOGICAL RACES OF THE BLACK SCALE, SAISSETIA OLEAE, AND THEIR SPECIFIC PARASITES[1]

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ABSTRACT

In California a race of *Saissetia oleae* (Bern.) was found with a unique capacity to attack commercial fig trees, and with other distinctive biological characteristics. Another race of *S. oleae*, imported from Mexico, was inhabited by a race of the common California encyrtid wasp *Metaphycus luteolus* Timb. which would not attack the ordinary California race of *S. oleae* but would attack its fig-infesting race. A series of interrelation tests on the two distinctive races of the parasite and the races of *S. oleae* confirmed their discrete biological identity. Adaptation of the imported race of the encyrtid to the local race of the scale insect could not be effected. The existence of taxonomically indistinguishable biological races of *S. oleae* was never suspected previously.

The collection and importation into California of the natural enemies of the black scale, *Saissetia oleae* (Bern.), has been one of the most intensive campaigns in the history of biological control. The foreign-exploration program has extended over five decades, and 68 primary parasites, 24 secondaries, and an uncounted number of predators have been recorded as attacking this pest.

In the course of the campaign there has never been any confusion as to the identity of this distinctively marked species of scale insect. There has, however, been some difficulty in arriving at a satisfactory explanation of the variability of plant hosts in different lands and climates, as

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well as the apparent unsuitability or lack of adaptation of certain imported parasites to the black scale, *Saissetia oleae*, attacking citrus, olives, and ornamentals in California. Where parasites presumably taken from *S. oleae* in a foreign land were found to be poorly adapted to that host in California, we generally attributed our inability to propagate the parasite species to mistaken host relationships. The following account of the discovery of taxonomically indistinguishable races of *S. oleae* that defy attack by parasitic Hymenoptera which readily develop on other scale races may help to explain some of the puzzling relationships encountered.

ACCESSION OF THE BLACK SCALE, *Saissetia oleae*, AND ITS PARASITES FROM MEXICO

In May 1954, samples of twigs and leaves of *Nerium oleander* infested with *Saissetia oleae* reached Riverside, California, in shipments sent by P. H. DeBach from the Mexican state of Tamaulipas. The collector's report indicated that citrus examined in that area was free of the scale. *S. oleae* was stated to be rare upon oleander and presumably held in check by a parasite which emerged singly from small scales and in larger numbers from scales up to mature size.

When received in quarantine at Riverside, the scale was immediately recognized as typical *Saissetia oleae*. From the samples received there emerged, from different stages of the scale, a total of 60 specimens of an encyrtid of the genus *Metaphycus*. The samples also contained a number of other primary parasites of the *Coccophagus lycimnia* (Wlkr.) complex, and hyperparasites of the genera *Marietta* and *Thysanus*. *Metaphycus* species emerged as solitary parasites from scale as small as 0.6 mm. in length and were progressively more gregarious in the larger scale, with as many as 10 inhabiting a mature host. Emergence was from small circular holes cut in the scale dorsum, and males and females occurred in approximately equal numbers. The species was identified by Harold Compere as *Metaphycus luteolus* Timb., and in living comparisons was found to be identical in all taxonomic characters with the common California species.

Metaphycus luteolus, as known in California, is a common and most efficient primary parasite, inhabiting all stages of *Coccus hesperidum* L. but attacking only a very narrow size range of *Saissetia oleae* (0.6 to 1.6 mm. in length). Therefore, it at first appeared likely that the new parasite represented a strain of *M. luteolus*, with a unique capacity for parasitizing all stages of the black scale. However, when the 60 specimens of *M. luteolus* from Mexico were tested against mixed stages of *Coccus hesperidum* and *S. oleae*, no reproduction occurred. The only possible explanations for the failure of this parasite to propagate on these hosts lay either in an unprecedented reproductive sterility of the parasites, or an equally unexpected specificity of the parasite to the Mexican race of *S. oleae*. With eventual loss of the import material, there was no opportunity for further examination.

DISCOVERY OF A DISTINCTIVE STRAIN OF *Saissetia oleae* IN CALIFORNIA

In 1955 the author's attention was called to a heavy infestation of *Saissetia oleae* on a commerical fig tree, *Ficus adriaticus*, in the Imperial Valley of California, 10 miles from the Mexican border. There was no previous record of this scale insect as a pest of commerical figs in California, although it has been so recorded in Texas and Arizona. The heavy infestation of black scale on *Ficus adriaticus* in the California desert was particularly unique because *S. oleae* is rare on other host plants in that area and presumably poorly adapted to the excessive heat. The scale on *Ficus adriaticus* was parasitized by the miscogasterid *Scutellista cyanea* Mots., as well as by the encyrtid *Metaphycus lounsburyi* (How.), the latter regarded as a highly specific parasite of *Saissetia oleae*.

Samples of the fig-infesting black scale were brought to the insectary quarantine for taxonomic and biological observation. Identification as *S. oleae* was established by the coccidologist Howard McKenzie. The scale grew readily on oleander but exhibited an unusual adaptability to growth and reproduction on citron melon (*Citrullus* sp.), a host plant which is ordinarily unsuitable for the development of continuous generations of the California citrus-infesting race of this scale insect. A host-plant race was indicated.

REINTRODUCTION OF PARASITES OF *Saissetia oleae* FROM MEXICO

Because of the promise of effective control offered by a race of *Metaphycus* with the potential of attacking all stages of *Saissetia oleae*, and in order to clarify the reasons for its failure to attack *S. oleae* in the initial import program, a second attempt to obtain the parasite was reinstituted in March 1957. The search was made by the author in the state of Tamaulipas, Mexico. The oleanders infested with *S. oleae* from which the original samples had been taken were by this time completely eliminated. Only a very few dead scale hulls remained, all of which showed the typical exit holes of *Metaphycus luteolus*. Further search in the vicinity finally revealed a very light infestation of living *S. oleae* upon a single oleander plant growing in the village of Carmen, about 1 mile from the original infested plants. From this plant, approximately 25 parasitized scales were obtained for shipment. A few unparasitized scales found beneath the soil level, where they were protected from parasitism, were included in the shipment as a host stock source for insectary quarantine, propagation, and examination. Shipment was made in cotton-plugged plastic tubes

heavily wrapped with slightly moistened paper for insulation against excessive temperatures. A few fine stripes of honey on the inside of the tube provided food for adults emerging en route. From this limited material a total of 26 living males and females of *M. luteolus* were obtained after receipt in California.

A continued intensive but fruitless search of the area for *Saissetia oleae* indicated its scarcity and confirmed the original observation that citrus was free from the scale. It was furthermore established that *S. oleae* attacked commerical fig in that area, although only remnants of previously parasitized scales could be found on a few dooryard trees. Significantly, also, no *M. luteolus* was obtained from the soft (brown) scale, *Coccus hesperidum* L., which was relatively abundant in the area.

BIOLOGICAL HABITS OF RACES OF *Metaphycus luteolus* AND *Saissetia oleae*

In the insectary, examination of the habits of the Mexican race of *Metaphycus luteolus* confirmed that this parasite would not develop upon the California race of *Saissetia oleae* (Bern.), nor upon *Coccus hesperidum* L., *C. pseudomagnoliarum* (Kuw.), or *S. hemispherica* (Targ.), all of which are readily attacked by the California race of the parasite. The Mexican *M. luteolus* was, however, easily cultured upon the California fig-infesting race of *S. oleae*, developing as a solitary parasite in the small scales and as a gregarious parasite in the large scales.

The unparasitized scales received from the Mexican shipment were transferred to oleander plants and cultured in quarantine. Their taxonomic status as *Saissetia oleae* was verified by three coccidologists. The adaptability of this race of *S. oleae* to citron melons further suggested its similarity to the distinctive race of the scale obtained from *Ficus adriaticus* in California. Subsequently, tests with the California race of *Metaphycus luteolus* on both the Mexican and the California fig races of *S. oleae* showed that this parasite was incapable of development on either, in contrast to its regular parasitization of the small stages of the California citrus-infesting race of black scale. This host specificity of the California race of the parasite therefore precluded contamination of the Mexican *M. luteolus* culture when maintained on either the Mexican or the California fig. scales.

TESTS ON ADAPTATION OF THE MEXICAN RACE OF *Metaphycus luteolus* TO THE CALIFORNIA BLACK SCALE

An ultimate adaptation of the Mexican race of *Metaphycus luteolus* Timberlake to the California citrus-infesting black scale was considered possible through mass exposure of the scale to large numbers of parasites. To test for adaptation, a sleeve cage was kept constantly stocked with 300 to 500 adults of the Mexican *M. luteolus*. A series of 42 potted oleander plants heavily infested with all stages of California black scale were exposed to parasite attack for periods of 3 to 4 days each and then removed to separate cages for surveillance as to parasite emergence. Only two plants were exposed at a time, so the process required over 2½ months. During this period, 35 female progeny of Mexican *M. luteolus* were obtained. The first 25 of this F_1 generation were placed, five each, directly upon a series of California scale-infested oleanders, but no further reproduction occurred. The last 10 F_1 parasites were propagated for one generation on the California fig race of *Saissetia oleae* on citron melons to assure their strain purity; their progenies were used to infest six separate plants heavily stocked with the California citrus-infesting race of *S. oleae*. Again, no progeny resulted. As a result of these tests, the host preference of the the Mexican race of *M. luteolus* is considered to be very inflexible.

The remaining insectary stocks of *Metaphycus luteolus* from Mexico were released in a test block of citrus that was heavily infested with *Saissetia oleae*. No indications of attack of large scales by the parasite have been found in the orchard.

DISCUSSION

The origin and racial segregation of both the distinctive race of *Saissetia oleae* and its specific parasite *Metaphycus luteolus* in Mexico afford interesting speculation. Specificity like that encountered presumably is indicative of a long-standing relationship between a host and its parasite. However, the *Saissetia* group is almost unquestionably of African origin, while the species *M. luteolus* does not occur in Africa, and is presumably confined to North America, except where purposely colonized for biological control purposes. The specificity and efficiency of the parasite against its host is therefore either an example of extraordinary effectiveness of a native parasite which has adapted itself to an imported host (which may be questioned in view of its absence on *Coccus hesperidum* in Mexico), or it must be supposed that both parasite and host were imported from a place of origin not conforming to our concepts of the native home of either species.

The discovery of a race of *Saissetia oleae* which is a potential pest on commerical figs in California makes its eradication desirable [when found in California], even though a parasite of high efficiency is available in Mexico for prospective introduction.

ECOLOGY OF THE IMMATURE STAGES OF SOME WISCONSIN BLACK FLIES (SIMULIIDAE: DIPTERA)[1]

JOHN R. ANDERSON AND ROBERT J. DICKE[2]

ABSTRACT

The immature stages of 23 black fly species, of the genera *Prosimulium*, *Cnephia*, *Eusimulium*, and *Simulium*, are here recorded from Wisconsin, 18 of them for the first time. Six other, unidentified species also were found, but their identification in most cases will await the discovery and association of pupal and adult stages. Notes on state distribution, relative abundance, and ecological relationships are presented for each species. The larvae were found to feed primarily on diatoms and other algae, some of which were scraped from the substratum. Waters containing large amounts of eroded soil particles and other detritus were unfavorable for most species, as the larvae appeared incapable of selective feeding and their intestinal tracts often contained more sand and silt than diatoms and algae; large soil particles were rejected, however, or perhaps were not small enough for ingestion. Microsporidian protozoans were common parasites of larvae, as was also a nematode, *Hydromermis* sp., which parasitized up to 90% of the black fly larvae in some streams. Larvae thus infested failed to pupate, and eventually died. The seasonal cycle of the nematode corresponded closely with that of *Simulium vittatum*; its larval stage was found parasitizing the overwintering larval populations of black flies in southern Wisconsin.

Prior to these investigations, the Simuliidae of Wisconsin were little known. Nicholson and Mickel (1950) reported two species of black flies in the genus *Simulium* Latreille that were collected in Sawyer and Shawano counties, and Roberts et al. (1956) listed three more species in the same genus collected from Rusk and Washburn Counties. From 1957 to 1959, 18 additional species were collected. The 23 species (table 1) now known represent the genera *Prosimulium* Roubaud, *Cnephia* Enderlein, *Eusimulium* Roubaud, and *Simulium* Latreille. Six additional species were found that did not fit any previously described larval or pupal stages. In most instances their specific determination awaits the discovery and association of pupal and adult stages and a study of their chromosomes. Except where they are mentioned as stream associates, these species will not be discussed.

Black fly adults exhibit wide dispersal ranges, often influenced by prevailing winds (Glick 1939; Underhill 1939; Rempel and Arnason 1947). Hence, where tiny streams and creeks are found in close proximity to larger rivers, it is difficult to base natural distribution (as determined by specific breeding sites) on collection records of adults. This investigation was undertaken to determine the black fly fauna of Wisconsin, and their distribution and relative abundance on the basis of collections of the immature stages from natural breeding sites.

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METHODS OF STUDY

Collections were taken from rivers and streams selected at random in 61 counties throughout Wisconsin. These collection sites were further localized by recording the section, range, and township of the counties in which they were taken. During 1957 and 1958, 274 larval and pupal collections were obtained from 199 different rivers and streams. Additional collections were obtained early in 1959.

At each study site particular attention was given to the following factors: topography of the terrain; width and depth, current velocity, turbidity, temperature, and substratum of the river or stream; types of substrata to which larvae and pupae were attached and their depths below the water surface; specific attachment sites on selected substrata; ratio of larvae to pupae; presence or absence of shade; and time of day collection was made. Current velocities were measured in feet per second with a glass pitot tube and by floating a cork or piece of wood in the current and timing it.

When the immature stages were attached to vegetation, small sticks, or other material that could be placed in a vial, specimens were preserved in 75% ethyl alcohol along with the substrata to which they were attached. Specimens attached to larger objects, such as large rocks or submerged branches, were removed with a forceps and placed in the preservative. Whenever mature pupae were present, a number were selected for rearing. Larval and pupal stages of various species were associated with one another by comparing the number of respiratory filaments. This was done by slitting the integument of mature larvae either just ahead of or behind the developing filaments. Pupal respiratory filaments were thus exposed so they could be counted and their pattern of branching compared with that of the pupae. The immature stages were identified largely with the aid of keys and descriptions by Twinn (1936), Stone (1952), Som-

merman (1953), and Stone and Jamnback (1955).

Population densities were estimated by counting the numbers present per selected square foot of substratum in streams where small populations were present. Where dense populations occurred, the actual numbers per square foot were estimated on the basis of a number of randomly selected square-inch counts. Thus it was possible to determine the relative abundance of the various associated species present in a specific habitat.

Table 1.—Species of black flies collected in Wisconsin from 1957 to 1959

Prosimulium (*Helodon*) *decemarticulatum* (Twinn)
gibsoni (Twinn)
(*Prosimulium*) *hirtipes* (Fries) complex
magnum Dyar and Shannon

Cnephia (*Cnephia*) *dacotensis* (Dyar and Shannon)
(*Stegopterna*) *mutata* (Malloch)
(*Ectemnia*) *taeniatifrons* (Enderlein)
Eusimulium aureum (Fries) complex
croxtoni (Nicholson and Mickel)
gouldingi (Stone)
johannseni (Hart)
latipes (Meigen)
pugetense Dyar and Shannon
Simulium (*Gnus*) *corbis* Twinn
(*Byssodon*) *meridionale* Riley
rugglesi Nicholson and Mickel
(*Simulium*) *decorum* Walker
jenningsi Malloch
luggeri Nicholson and Mickel
tuberosum (Lundstroem)
venustum Say
verecundum Stone and Jamnback
(*Neosimulium*) *vittatum* Zetterstedt

Water samples for analyses were collected in standard 2½ liter bottles used by personnel of the Wisconsin State Laboratory of Hygiene for obtaining water samples from rivers and streams. Half of each sample was separated for chemical analysis and determination of total and suspended solids present, while the suspended matter in a known portion of the remainder was concentrated on a membrane filter and the kinds and number of phytoplankton organisms per milliliter of water were determined according to the procedures of McNabb (1960).

Two methods were used to analyze the intestinal contents of larval specimens. The first of these was a microscopic analysis in which the dissected intestinal tracts were removed, placed on a glass slide, and then squashed with a coverslip. Percentages of various components in the intestines were then estimated from observations on several areas of each intestinal tract. A second technique employing the ignition method of analysis was carried out mainly to serve as a check on the reliability of the microscopic examination to detect accurately the amounts of sand and soil granules (such as silt and clay) in the contents of larval intestines. Using this technique, all adhering tissues were removed from the intestinal tracts, and the intestines were ignited in a crucible. In this manner, the total fixed and volatile solids (representing inorganic and organic matter) were determined.

CLASSIFICATION AND DISCUSSION OF STREAM TYPES

During these investigations various species of simuliids were found only in specific types of flowing water. It follows then, that some sort of river and stream classification is advantageous in a discussion on the ecology of the immature stages. A general discussion of the major types of rivers and streams found in Wisconsin follows.

A. Temporary Flowing Water

1. Bog Seeps.—These are small channels generally no wider than 6 inches nor more than 1 inch in depth. They are found throughout the northern forested regions of the state and are characterized by sod substrata and dead grasses trailing in the current. The immature stages are attached to the grasses. These tiny streams are usually not more than one-half mile in length, and are present for approximately 1 month of the year during April or May.
2. Drainage Creeks.—These range in size from 6 inches in width near the source to about 3 to 4 feet where they flow into larger permanent streams. Their depths may vary from 1 to 2 inches to about 12 inches. The stream beds vary somewhat depending on the region of the state and the topography of the land, but most consist largely of sand, small stones, and a few large rocks. Their maximum life is about 5 months and most are dry by mid-June. These streams are generally 2 to 5 miles long. They either empty into lakes or are tributaries of larger streams or rivers.

Both types originate from melting snow during the spring of the year.

B. Permanent Flowing Water

The following classification is adapted from Dalmat (1955), and the terms "young" and "old" refer to the morphological "age" of the river or stream rather than the geological "age". Individual river and stream characteristics apply to Wisconsin area waters.

1. Young Streams.—These generally range from 2 to 10 feet in width and 6 inches to 3 feet in depth. The substrata in these clear streams consist largely of a mixture of gravel, rocks or small boulders. The water flowing over the rocks and boulders frequently forms small waterfalls and rapids, so that their current velocities here are characteristically faster than 3 feet per second. Water temperatures rarely exceed 60° F. These streams eventually empty into larger bodies of water.
2. Old Streams.—These streams vary from

Table 2.—Food and stream factors affecting species composition of various waters.

Sample source	Current velocity (f.p.s.)	Total solids (p.p.m.)	Suspended solids (p.p.m.)		Organisms/ml.		5-day B.O.D.	pH	Total organic nitrogen (p.p.m.)	Black fly species
			Fixed	Volatile	Diatoms	Algae				
Pheasant Branch Creek	0.2–0.5	774	18	40	7681	296	277.0	7.0	11.4	*S. vittatum*
Twinn Lake Creek	1.0–1.5	408	2	3	None	337	4.4	7.85	1.80	*C. dacotensis*
Black Earth Creek	1 –2	372	60	8	1724	None	3.2	8.15	0.80	*S. vittatum*
Puchyan River	1.5–5.0	244	4	2	84	20	3.6	8.95	0.60	*E. aureum* *S. venustum* *S. decorum* *S. vittatum*
Tributary of Baraboo River	0.5–2.0	102	12	6	145	66	2.5	7.5	0.43	*C. dacotensis* *P. magnum* *S. tuberosum* *S. venustum*
Otter Creek	2.0–5.0	58	1	1	100	None	1.3	7.5	0.09	*P. hirtipes* complex *P. magnum* *E. aureum* *S. tuberosum* *S. venustum*

3 to 15 feet in width and about 1 to 4 feet in depth. The stream beds consist largely of mud, but may occasionally have small amounts of sand or gravel mixtures. Larger rocks may be present but are infrequent. Aquatic vegetation is sometimes quite prominent. The topography of the land through which these streams flow is of a gentle rolling nature. They are almost always found in cleared and cultivated agricultural areas of the state. These are sluggish flowing streams whose current velocites are usually less than 3 feet per second. They are characteristically "muddy colored" as a result of large amounts of silt particles carried along by their currents.

3. Young Rivers.—These may vary in size from about 10 to 50 yards wide and about 1 foot deep along the banks up to depths greater than 5 feet elsewhere in the channels. Their substrata are characterized by large rocks, boulders and gravel. Rapids and various sized waterfalls are common. These clear, cold rivers are generally regarded as good "trout waters". They are largely restricted to the rugged, forested terrain in the northern regions of the state.

4. Old Rivers.—These are slow flowing, muddy-colored rivers, which are usually greater than 50 yards in width and attain depths up to 10 feet or more. The stream beds are usually soft and muddy, and frequently support submerged logs and dead trees. Immature populations of black flies are most commonly encountered attached to rocks, submerged branches, and vegetation on sand bars and along the banks.

NUTRITIONAL ASPECTS

Large cephalic fans are used by the larvae to strain microscopic food particles from the water. These fans can either be expanded and held stationary in the current, or moved back and forth towards the mouth of the larvae. The larvae are also able to obtain food by scraping the area around the substrata to which they are attached. Peterson (1956) reported on the method of feeding for *S. vittatum* and the intestinal contents of larvae from two streams in the mountains near Salt Lake City, Utah.

Results of a study to determine the types of food available for larvae, and other stream factors that might effect the species composition in several Wisconsin streams are included in table 2. All water samples included in this table were collected on the same date (May 14, 1958) between the hours of 10:30 a.m., and 3:00 p.m.

The suspended solids represent organic matter in the water samples plus particles of sand, clay, and silt carried along in suspension. Total solids represent the suspended solids plus the normal chemical composition of the water such as carbonates, nitrates, chlorides, and metallic ions carried in solution. From table 2, it is seen that the three creeks which had the largest amount of total solids were also limited to a homogeneous population of one species of black fly larvae. A comparison of the fixed and volatile portions of the suspended solids in these streams indicates that Black Earth Creek carries large amounts of eroded soil particles and other detritus in suspension. This is a relatively slow-moving creek of the old-stream type that flows through a gently rolling terrain in the agricultural region of southern Wisconsin.

FIG. 1.—Distribution of certain species of black flies in Wisconsin. All other species occurring here have a statewide range.

1, *P. decemarticulatum*; 2, *E. croxtoni*; 3, *E. pugetense*; 4, *E. johannseni*; 5, *S. corbis*; 6, *S. luggeri*; 7, *S. meridionale*; 8, *S. rugglesi*.

The three streams containing the smallest amounts of total solids also had the greatest number of species present. Of these streams, the tributary of the Baraboo River is representative of a temporary drainage creek; Otter Creek represents a permanent, flowing, young stream; and the Puchyan River is characteristic of the young river. As evidenced by its extremely high 5-day biological oxygen demand, Pheasant Branch Creek was found to be highly polluted. The larval population was extremely small, and it seemed somewhat suprising that larvae were present at all.

Streams carrying large amounts of eroded soil particles and other detritus are unfavorable habitats for most species of black flies because the suspended particles may interfere with larval feeding. Davies (1958) suggested that a low tolerance for the mechanical action of these larger particles in rivers and streams may also be partly responsible for the reduced species composition in streams carrying large amounts of eroded soil particles and other detritus. Certain species, such as *S. vittatum*, appear to tolerate large amounts of debris carried along by the current in streams, this is suspected to account in part for the abundance and statewide distribution of the species. Other species apparently are restricted from certain types of streams because of their low level of tolerance for large amounts of these particles in muddy streams, although other factors such as water temperatures, available

Table 3.—Diatoms and other algae present in water samples[a]

Diatoms	Sample sources[b]					
	I	II	III	IV	V	VI
Cocconeis spp.	216		88	29		
Cyclotella spp.				7	43	22
Cymbella spp.						29
Diatoma spp.						13
Fragilaria spp.				12	14	
Gomphonema spp.			252	3	14	6
Melosira spp.				3		5
Meridion spp.					5	8
Navicula spp.	104		1084	20	69	4
Nitzschia	7325		56			7
Rhoicosphenia spp.				3		6
Surirella spp.			140			
Synedra spp.	36		104	7		
Other Algae						
Ankistrodesmus spp.				4	40	
Chlamydomonas spp.	36				5	
Coelastrum spp.		3				
Cryptomonas spp.				7		
Euglena spp.	260			3		
Scenedesmus spp.		51		6		
Pediastrum spp.		3				
Trachelomonas spp.		280				
Tribonema spp.					21	
Total Organisms	7977	337	1724	104	211	100

[a]Arabic numbers represent organisms per milliliter.
[b]Roman numerals represent order of sample source appearing in table 2, i.e., IV represents the Puchyan River.

food stuffs, and hosts of the blood-sucking adults also act to influence species distribution and abundance.

The contents of larval intestinal tracts of specimens collected from these various streams were studied to determine if larvae were selective in filtering food particles from the water, and to determine the amount of soil and sand ingested. Diatoms and other algae found in water samples are presented in table 3. All species of larvae examined from a given stream were found to contain all organisms present in the water sample from that stream.

Table 4 gives percentages of various components in the intestines as determined by the microscopic method of analysis, and also lists diatoms and other algae which were found in the intestines but were not collected in the water samples. The presence of the latter organisms in the intestinal contents indicates roughly which species of phytoplankton the larvae obtained by scraping the substrata. For example, the data in tables 3 and 4 for the Tributary of the Baraboo River show that although the diatoms *Rhiocosphenia* spp. and *Cocconies* spp. were found present in the intestinal contents, these two organisms were not obtained in the water sample taken from the creek. Large aggregations of these species are commonly found growing on rock surfaces in many streams. The larvae are capable of scraping some of these organisms from their attachment sites and then ingesting them. To distinguish them from the organic food material, the various sizes of soil particles and mud in table 4 are treated as inorganic matter, although it is recognized that small amounts of organic matter were also undoubtedly present in these particles.

In the process of microscopically analyzing intestinal contents, diatoms were not considered as contributing to the fixed (inorganic or soil) portion of the total contents. Examination of residues following ignition showed that the diatom frustules remained and therefore contributed to the fixed solids. This contribution to the inorganic or soil portion of the total contents tended to be cancelled out by the thin intestinal lining and organic matter in the soil granules being volatilized and contributing to the volatile solids. Table 5 contains results obtained by the

Table 4.—Microscopic analysis of intestinal contents of larvae.

Collection site	Species	Organic matter[a]			Inorganic Matter
		Diatoms	Other algae	Misc.	
Twinn Lake Creek	*Cnephia dacotensis*	*Navicula* spp. *Cylotella* spp. *Melosira* spp. (1%)	*Scenedesmus* spp. *Oocystis* spp. *Chodatella* spp. *Golenkinia* spp. *Spirogyra* spp. (39%)	None	Small soil granules with a few large sand grains. (60%)
Otter Creek	*Prosimulium magnum*	*Cocconeis* spp. *Synedra* spp. (45%)	*Tribonema* spp. *Cosmarium* spp. (2%)	Higher plant remains;[b] fungal filaments. (5%)	Much sand with some small soil granules. (48%)
	Simulium venustum	(29%)	*Tribonema* spp. (1%)	Same as above Filamentous fungi rare (8%)	Same as above (62%)
Black Earth Creek	*Simulium vittatum*	(13%)	*Oscillatoria* spp. (1%)	Higher plant remains. (1%)	Soil granules (85%)
Trib. of Baraboo River	*Prosimulium magnum*	*Cymbella* spp. *Synedra* spp. *Rhoicosphenia* spp. *Diatoma* spp. *Amphora* spp. *Cocconeis* spp. *Nitzschia* spp. (42%)	*Spirogyra* spp. (1%)	Higher plant remains; fungal spores and filaments rare (10%)	Sand and small soil granules (47%)
	Simulium tuberosum	*Nitzschia* spp. *Diatoma* spp. *Rhoicosphenia* spp. *Cocconeis* spp. (10%)	(5%)	Same as above (5%)	Large and small soil granules and sand (80%)
Puchyan River	*Simulium vittatum*	*Nitzschia* spp. (12%)	*Euglena* spp. *Oocystis* spp. *Phacus* spp. (37%)	Bits of chitinous invertebrate body "shells" and tips of appendages; fungal filaments rare. (1%)	Sand and small soil granules (50%)
	Simulium decorum	*Nitzschia* spp. *Surirella* spp. (19%)	*Oocystis* spp. *Spirogyra* spp. *Ankistrodesmus* spp. *Euglena spp.* *Oscillatoria* spp. *Coelastrum* spp. (35%)	Same as above (1%)	Same as above (45%)

[a]The diatoms and other algae present in addition to those found in the respective water samples.
[b]Includes leaf fragments, woody fibers, etc.

ignition method of analyzing larval intestinal contents.

The data of tables 4 and 5 are in close agreement when one considers the above points. For example, microscopic analysis of intestinal contents from Black Earth Creek showed 85% of total contents to be inorganic matter, whereas diatoms composed 13% of the total contents. The ignition method showed 76% inorganic and 24% organic. The 9% difference in the two methods can be explained by the fact that the 85% soil granules estimated by the coverslip technique probably contributed more organic matter to the volatile solids than the 13% diatoms contributed to the fixed solids.

From a comparison of the data in tables 2 and 5 it is seen that the amount of eroded soil particles and other detritus in larval intestines varied considerably, depending on the type of stream in which larvae were found. It is apparent that larvae fed almost wholly on diatoms and other algae. Additional observations on intestinal contents from larvae collected in other rivers and streams in Wisconsin are given in table 6. The species collected from the larger rivers were found to contain only small percentages of soil granules and sand, whereas those found in small forest streams contained large amounts of soil.

The data in tables 2 and 4 indicate that larvae are partially selective in their method of straining food particles from the water, i.e. larger particles

of eroded soil particles and other detritus carried along in the currents were either rejected or were too large for the larvae to ingest. All species studied were found capable of ingesting tiny particles of sand, clay, and silt in suspension. One might suspect this on the basis of the data given in tables 3 and 4, as the structure and chemical composition of sand grains is indeed quite similar to the silicous shells of diatoms. With suspended solids, the larvae did not appear to be capable of selective feeding. Thus, in the streams with the larger amounts of sand, clay, and silt in suspension, the intestines were found to contain more of these tiny particles than diatoms, other algae, or other plant or animal foodstuffs. It was also observed that the dominant organisms present in the water sample from a given stream were also the most common constituents of the food material in the intestinal contents.

CROWDING EFFECTS

Under natural river and stream conditions the primary competition among the larvae is for specific attachment sites on selected substrata. Even where available substrata for attachment sites appear almost infinite (i.e., extremely rocky rivers or streams containing abundant vegetation) homogeneous populations of larvae are usually found aggregated only at specific sites on the rocks or vegetation. Successful attainment of a favorable site in turn influences such factors as the kinds and amount of food ingested, rate of growth, protection from enemies, and shelter from adverse physical effects of the environment.

In certain parasite- and predator-free populations where limited substrata occur, the larval populations are found in tremendous numbers in respect to the substrate area. Sites have been investigated in which every blade of grass trailing in the water was completely covered with larvae on both the upper and lower surfaces. At one such site, grass blades ½ inch wide and 6 inches long supported from 300 to 800 *S. vittatum* larvae. In other streams in which rocks served as the substrate, as many as 2,000 to 4,000 *P. hirtipes*-complex larvae were attached to individual rocks about 10 to 12 inches in diameter. Metcalf (1932) reported counts of 2880 larvae on one rock and 1500 larvae on another, but did not indicate the size of the rocks. He further reported finding 300 larvae per square foot in a tiny brooklet near an Adirondack hotel. Sommerman et al. (1955) recorded maximum population counts as high as 250 to 6,000 larvae per square foot of selected substratum at semi-upland collection sites in Alaska, and 2,500 to 15,000 at lowland stations.

Evidence that the majority of larvae in Wisconsin streams survived under the above crowded conditions was obtained when comparable numbers were found present at later investigations. Pupal cocoons were then present on almost every inch of available substrate and many of these were constructed one on top of the other or adjacent to each other so that they were several layers thick. The larvae present were attached to parts of the normal substrate (rocks or vegetation) and also to the pupal cases. The principal adverse effect on the developing larval populations in these crowded sites was a reduction in the size of the individuals rather than a reduction in numbers of individuals. However, the overall deleterious effects of development in these overcrowded situations appears to be a reduced fecundity and a high mortality rate among the stunted adult populations.

PARASITES AND PREDATORS

In virtually all rivers and streams the larval populations were held somewhat in check by many natural enemies which prevented them from reaching the tremendous numbers previously cited. Perhaps the most important enemy in Wisconsin is a mermithoid nematode of the genus *Hydromermis* which was found in 10% of the study areas. Where it occurred, this parasite often infested more than 50% of the larvae.

The nematode larvae inhabit the body cavities of simuliid larvae and are usually coiled in the larger, posterior portion of their hosts' bodies. At other times, the nematodes may be somewhat elongated, stretching the entire length of their hosts. Superparasitism was common. The body of a parasitized larva consisted largely of a cuticular shell harboring the parasite. Infestation by these nematodes prevented the host larvae from pupating and eventually led to their deaths.

Parasitism of simuliid larvae by mermithoid nematodes was first reported by Strickland (1911, 1913), who found them present in a small percentage of larval populations near Boston. Other workers who have reported on mermithoid parasites of black fly larvae are Twinn (1936, 1939), Hocking and Pickering (1954), Dalmat (1955), and Sommerman et al. (1955).

Both Hocking and Pickering (1954) and Dalmat (1955) reported that nematode parasitism of the larvae did not always prevent pupation. Hocking and Pickering (1954) reported finding a mermithoid worm infesting a *S. venustum* pupa in a laboratory colony and also finding two worms in a *S. venustum* adult female. Dalmat (1955) also found nematode parasites in adult flies.

The nematode occurring in Wisconsin probably is a different species than those reported from other areas, as the evidence obtained in these investigations indicates that all larvae infested with mermithoid worms are prevented from pupating and eventually die. The evidence consists of the following:

(1) This nematode worm prevented the development of the pupal and adult histoblasts (in mature healthy larvae, the pupal histoblasts of the

Table 5.—Analysis of larval intestinal contents by ignition method.

Collection site	Species	Instars	Number examined	Total dry weight	Fixed solids	Volatile solids
Black Earth Creek	*S. vittatum*	3rd and 4th	13	3.3 mg.	2.5 mg. (76%)	0.8 mg. (24%)
Trib. of Baraboo River	*P. magnum*	4th	9	2.3 mg.	1.3 mg. (57%)	1.0 mg. (43%)
	S. tuberosum	6th	4	1.4 mg.	1.0 mg. (71%)	0.4 mg. (29%)
Puchyan River	*S. vittatum*	5th	9	1.3 mg.	0.6 mg. (46%)	0.7 mg. (54%)
	S. decorum	5th	9	1.4 mg.	0.7 mg. (50%)	0.7 mg. (50%)
Twinn Lake Creek	*C. dacotensis*	4th and 5th	9	1.7 mg.	1.1 mg. (65%)	0.6 mg. (35%)
Otter Creek	*P. magnum*	4th	4	1.7 mg.	1.0 mg (59%)	0.7 (41%)
	S. venustum	4th	4	1.0 mg.	0.7 mg. (70%)	0.3 mg. (30%)

respiratory filaments and adult histoblasts of the legs, wings, and halteres are quite prominent in the proleg region). Thus parasitized larvae could not metamorphose to the pupal stage without the necessary organs for respiration, nor to the adult stage without development of legs, wings, and halteres. In all parasitized larvae examined from Wisconsin, histoblasts of the pupal respiratory filaments consisted merely of tiny, light-colored masses of a gelatinous substance and there was no evidence of filament formation. Adult histoblasts were darker in color but extremely underdeveloped and almost nonexistent in comparison to those of normal mature larvae;

(2) Nematodes were never observed in pupae collected from populations containing parasitized larvae;

(3) The proportion of larvae to pupae present in populations at the study areas was found to approximate the proportion of the percentage of larval populations that were parasitized. Table 7 shows the relationship between the percentage of parasitized larvae and the proportion of larvae to pupae present in five of the study areas where the nematode parasite was most abundant in 1957.

Strickland (1911, 1913) and Twinn (1936, 1939) both reported comparatively lower percentages of parasitism, but Hocking and Pickering (1954) reported that by the last week in July, diseased larvae outnumbered the healthy ones; and Sommerman et al. (1955) have reported that 65% of a *S. tuberosum* population estimated to be 1,500 larvae per square foot were found parasitized by a mermithoid nematode of the genus *Limnomermis*. All these workers studied the parasite during the spring and summer months, except Twinn, who found them present in larvae as late as September.

The seasonal cycle of the mermithoid parasite in Wisconsin evidently corresponds closely to that of the black fly *S. vittatum*, as its larviform stage was found parasitizing overwintering populations of larvae in a number of southern Wisconsin streams. From several small collections made on February 5, 1958, it was determined that 5% of the larval population in Black Earth Creek were parasitized on that date. In February 1959 it was determined that 8% of the overwintering *S. vittatum* larval population were parasitized. Mode of entry into the larval host and the life cycle of the worm are not known.

However, from an analysis of several parasitized populations composed of a number of different instars, it appears that simuliid larvae either ingest the eggs of this parasite while feeding, or that the larval nematodes penetrate the integument of their hosts. An example of a parasitized population in which 15% of the larvae were found to contain one or more nematodes is given in table 8. This sample was obtained from the Red Cedar River in Barron County, where the immature stages were found attached to aquatic vegetation and small rocks in a wide, rocky, shallow area of the river approximately 30 feet out from the bank. Water depths ranged from 12 to 18 inches, but most of the larvae were attached from 2 to 6 inches below the surface.

The incidence of increased parasitism in the intermediate larval instars of such populations indicates that transmission of the nematode occurs by the larvae becoming infested. The decrease of parasitism in later instars probably represents mortality due to nematode infestations. The following laboratory observations lend support to this hypothesis.

On July 16, 1959, approximately 400 *S. vittatum* larvae (of which 20% were parasitized) were placed in a series of small enameled pans supplied with compressed air. Fifteen parasitized larvae were separated and placed in one of the pans (pan #1). The remaining pans contained both

Table 6.—Additional Intestional observations[a]

Species	Habitat & coll. date	Intestinal contents
P. decemarticulatum	Temporary bog seep in northern forest region 5/9/58	Approx. 50% dark-colored soil particles; diatoms dominant plant material; some filamentous algae present; gut loosely packed.
C. mutata	Old stream in northern forest region—5/11/58	Approx. 50% soil granules; diatoms 30%; filamentous algae 10%; wood fibers, leaf fragments & head capsule 10%; gut tightly packed.
E. pugetense	Old stream in northern forest region—5/10/58	Approx. 65% soil granules; diatoms 20%; filamentous & colonial algae 10%; wood fibers & leaf fragemnts 5%; gut moderately packed.
S. jenningsi	Young river in central farming region—5/18/58	Approx. 10% sand & soil particles; diatoms 10%; algae 78%; higher plant fibers & head capsule 2%; gut tightly packed.
S. luggeri	Young stream in northern forest region 5/24/58	Approx. 5% sand & soil particles; diatoms 30%; algae 65%; few woody fragments; gut loosely packed.
S. luggeri	Young river in northern forest region—5/23/58	Approx. 5% sand & soil particles; diatoms 90%; filamentous algae 5%; gut moderately packed.

[a]Microscopic method of analysis

parasitized and nonparasitized larvae. Finely ground protein pellets served as a source of food. In addition, diatoms and other algae may have been obtained from vegetation that had served as the substrate in the normal habitat and which was introduced into several pans.

All parasitized larvae contained in pan #1 were dead after 5 days. The first fatalities were noted on July 20, at which time 5 of the parasitized larvae were dead. Seven nematodes were observed freely moving about at the bottom of the pan. At this time 5 nonparasitized larvae were introduced into the pan containing the nematodes and remaining parasitized larvae. On July 22, all parasitized larvae were dead and about 20 nematodes were moving about on the bottom of the pan. Examination of dead larvae showed that histoblast development had been suppressed. Most nematodes had apparently gained their exit by rupturing the integument of their hosts' bodies, but some of the dead black fly larvae examined showed no evidence of physical damage inflicted to their bodies. Nematodes did not enter the bodies of nonparasitized larvae introduced on July 20. Two of these larvae pupated on July 22, and one was dead on this date. The remaining two nonparasitized larvae had pupated by July 27. Adults subsequently emerged from all the pupae. Larval development in the remaining pans was normal.

Table 9 lists the species of black fly larvae found infested with nematodes during this study.

Other common parasites of larvae are microsporidian protozoans, but these are sporadic in their distribution and affect only small numbers of the overall populations where they occur. These parasites usually cause the deaths of the larvae. Parasitized individuals can be easily recognized by the appearance of large, thick, white masses of spores packed within the body or by bluish-tinted spores on the outer integument. Occasionally some pupae were parasitized by microsporidian protozoans, but the incidence was low. No other pupal parasites or predators were observed. Davies (1956) reported on various microsporidian parasites in eastern Canada and found them to be of minor importance in controlling black fly populations in that area.

Predaceous species of fish and insects consume a portion of the larval populations. Some of the more important insect predators are mayfly and stonefly naiads, and larvae of certain chironomids and caddis flies. Most of these predators were inhabitants in the same streams as black fly larvae, but it was not ascertained what percentage of the total larval population they consumed. Sometimes chironomid larvae were found sharing the pupal cocoon, but apparently caused no ill effects to the pupae.

DISTRIBUTION, RELATIVE ABUNDANCE AND ECOLOGICAL RELATIONSHIPS OF WISCONSIN FAUNA

It is now known that 15 of the 23 species occurring in Wisconsin have a statewide distribution. Of the remaining eight species, six appear to be restricted to the northern forest regions of the state and two have been found to occur primarily in the southern agricultural areas. Individual species distributions are shown in figure 1.

Prosimulium (*Helodon*) *decemarticulatum* (Twinn).—This species is moderately common and widespread throughout the northern forest region of the state, where immature stages have been found in bog seeps, forest drainage creeks, and young streams associated with swampy forest areas.

Larvae collected from tiny, partially underground streams draining from a forest bog into a small river were found in association with *Cnephia*

Table 7.—Relationship of nematode parasite in preventing pupation.

Collection site	County	Date	Percentage of parasitized larvae	Proportion of larvae to pupae	Species
Moose Ear Creek	Barron	6/25/57	50	60–40	*S. tuberosum* *S. venustum*
Black Earth Creek	Dane	8/2/57	80	95–5	*S. vittatum*
Little Platte River	Grant	8/21/57	55	60–40	*S. vittatum*
Camp 4-Creek	Ashland	8/29/57	50	95–5	*S. tuberosum* *S. venustum* *S. vittatum*
Small unnamed Creek	Bayfield	8/30/57	85	95–5	*S. venustum* *S. vittatum*

species # 1. Both species were attached to dead grasses in current velocities of less than 1 foot per second. A thorough search of the river yielded no specimens. Second- and third-instar larvae were collected from these bog seeps on May 9, 1958, at which time the water temperature was 34° F. In different areas of these tiny trickles of water the number of *P. decemarticulatum* larvae ranged from 1 to 5 per square foot and made up about 80% of the total larval population.

In forest drainage creeks, *P. decemarticulatum* composed 2% to 11% of the total populations, and was associated with *Cnephia* species # 2, *Cnephia mutata*, *E. gouldingi*, and *S. venustum*. During May, water temperatures in this type of habitat ranged from 48° to 61° F. At temperatures rising from 51° to 55° F. larvae were found to develop from fourth and fifth instars to the sixth instar and pupal stage in 7 days. The pupal stage required from 4 to 6 days.

Development in young streams was similar to that occurring in drainage creeks. However, populations were slightly larger and consistently more uniform in size in the young streams where *P. decemarticulatum* larvae and pupae were found at 100 to 300 per square foot of selected substrata, and generally made up 12%–15% of the total immature populations. In both types of streams the preferred sites of attachment were on grasses trailing in the current. Other substrata utilized were rocks and submerged branches.

In 1959, pupation occurred between May 10 and May 20, in all streams investigated. There is a single generation a year in Wisconsin.

Prosimulium (*Helodon*) *gibsoni* (Twinn).—This species has been collected in several widely separated areas of the state. Larvae have been collected only in small usually rocky, semipermanent streams of the temporary drainage creek type that are usually dry by early June. Water temperatures of these streams varied from 58° to 68° F. during late April and May, 1958. In Manitowoc County, larvae were present in small streams flowing into Lake Michigan. Here they were associated most often with *C. dacotensis* but also occasionally with *S. venustum*. In all these streams, *P. gibsoni* made up only a tiny portion of the total larval populations, which ranged from 50 to over 1,000 per square foot of selected substratum. Their numbers ranged from less than 0.5% in some streams to a high of 1.4% in others. Larvae were attached to small rocks or grasses trailing in current velocities of about 0.5 to 1.5 feet per second.

As evidenced by the following, *P. gibsoni* is apparently not able to tolerate environmental conditions in which large amounts of eroded soil particles and other detritus are present in streams. A mixed population numbering 200 to 500 larvae per square foot of rock surface and consisting of 20% of third and fourth instars of *P. gibsoni* and 80% *S. venustum* was found in a clear, rocky, semipermanent stream in Sauk County on April 23, 1958. A week later, under muddy stream conditions, the population at this site consisted only of *S. venustum* larvae. During the time between the two investigations, a herd of swine had been turned into a pasture just upstream from the collection station. This action was responsible for the muddy stream conditions existing on May 1. Upstream from the hog pasture, a *P. gibsoni* population which had not yet begun to pupate was present in clear water. However, at the collection station downstream from the hog pasture, the *P. gibsoni* population had completely disappeared while the *S. venustum* population was progressing normally and subsequently went on to pupate and emerge as adults.

This is an early spring species which occurs only in small numbers throughout its distribution range. In addition to *C. dacotensis* and *S. venustum*, *P. gibsoni* was also found associated with *P. magnum*, *C. mutata*, *E. gouldingi* and *E. latipes*. There is one generation a year in Wisconsin. The eggs are apparently able to resist desiccation, as they lie in a dormant state in dry stream beds from early June until early April of the following year.

Prosimulium (*Prosimulium*) *hirtipes* (Fries) complex.—This complex of species has the widest range for members of the genus *Prosimulium* in

Wisconsin. Although statewide in distribution, it is particularily abundant in the northern areas of the state.

In Wisconsin "*P. hirtipes*" consists of a complex of at least three very closely related species which are similar in their morphological characteristics and ecological requirements. Populations of two and sometimes three species occur in similar type streams. One of the members of this complex (the species with the largest larva) consistently matures several days before the other members in the streams, but overlapping of maturing populations confuses the species complex.

Table 8.—Mermithid parasitism of a population[a] of *Simulium luggeri*.

Instar	Total no. coll.	No. parasitized	Percent parasitized
Second	558	8	0.014
Third	562	129	23.10
Fourth	186	53	28.50
Fifth	97	19	19.60
Sixth	19	1	0.066
Pupae	16	0	0.00
Total larvae and Pupae	1422	210	14.77

[a]Collection date—5/24/58, Red Cedar River, Barron County.

Syme and Davies (1958) and Davies and Syme (1958), working primarily with material from Eastern Canada, separated the species formerly known as *P. hirtipes* into three species. This was possible on the basis of micromorphological and ecological studies following Rothfels' (1956, 1958) discovery that the species formerly called *P. hirtipes* in Eastern Canada actually consisted of a complex composed of at least three cytologically distinct species. Rothfels (1958) further determined that these three species all differ cytologically from *P. hirtipes* from Northern Europe. Syme and Davies (1958) showed that the name *P. hirtipes* should apply only to the Northern European species, and have not used the name *hirtipes* for any of the three species formerly recognized in the *P. hirtipes* complex in Eastern Canada.

Because of the lack of cytological material and complete series of larvae, pupae, and adults from all areas of the state, and because the name *P. hirtipes* has formerly been widely recognized, the species in the paper are presently treated as members of the *P. hirtipes* complex.

This complex contains the most abundant and troublesome early spring species of black flies in Wisconsin. The immature stages are commonly found in clear, cold, rocky streams typical of the northern forest area of Wisconsin and nonagricultural areas in the southern region of the state. These streams are characteristic of the young stream type. The period of larval development requires several months, and tremendous numbers of overwintering larvae are present in streams throughout the winter months. This long period of larval development is probably related to low water temperatures and scarcity of food.

Water temperatures vary from 32.5° to 60° F. during development and maturity. Pupation normally occurs after the streams have warmed up to above 40° F. The pupae of the first maturing species of this complex occur on the upper and downstream surfaces of rocks where they are found in dense, gummy masses often composed of several layers of pupae. The pupae of the second and third species of this complex are not found in such large masses but are more evenly dispersed throughout the streams. The pupal stage required about 6 to 9 days at water temperatures from 40° to 50° F.

In all streams from which members of the complex have been collected, rocks were the preferred substratum. The most common sites of attachment were on the sides and downstream surfaces. Occasionally specimens have been collected on submerged branches and leaves. The immature stages are rarely found on grasses or other types of vegetation.

The complex, like other species of *Prosimulium* in Wisconsin, has one generation a year. It contains some of the earliest species of black flies that occur in the spring. Mature larvae and a few pupae were collected as early as March 26, 1958, from Otter Creek in Sauk County. Adults were observed for the first time at this site on April 9, 1958, at which time 30% of the total population numbering 500 per square foot of rock surface had pupated. Pupation in the northern counties occurred about a week later and adults were on the wing during the last week in April and early May following a mild winter.

Larvae and pupae are usually present in enormous numbers (populations varied from less than 50 to over 2,000 per square foot of selected substrata in various streams) in swift rocky areas of streams; these large populations create a favorable situation for the development of parasites. Microsporidian infections of black fly larvae are generally considered to be of minor importance, but in one northern stream (Armstrong Creek in Forest County) 95% of a larval population were diseased. However, at this time 75% of the total population had pupated and 50% of the pupal population had emerged, so that a much smaller percentage of the total population was held in check by the parasite. The total population of larvae and pupae in the area was estimated to be 2,000 per square foot.

Eggs are deposited freely into the water where they sink to the bottom of the streams. They remain dormant there until they hatch during the early winter months. In a number of streams,

immature stages were found to constitute a homogeneous population of the complex. In others, *P. magnum* and *S. vittatum* were found associated with the complex in various sections of its southern range. In northern regions, *C. mutata*, *S. corbis*, *E. pugetense*, and *S. venustum* were the common associates. Of these associated species, *C. mutata* and *S. vittatum* were at the same stage of development.

Prosimulium (*Prosimulium*) *magnum* Dyar and Shannon.—Although this species has a statewide distribution it is more frequent and occurs in greater numbers in central and northern Wisconsin than in the southern region of the state. The immature stages are most commonly found in temporary drainage creeks that become dry in early June and remain so until the following spring.

Table 9.—Species found infested with nematodes. (1957–1959)

P. decemarticulatum	*S. corbis*
P. gibsoni	*S. luggeri*
P. hirtipes complex	*S. tuberosum*
P. magnum	*S. venustum*
C. mutata	*S. vittatum*
E. latipes	*Simulium* sp. No. 1

Water temperatures of temporary streams in which this species occurred ranged from 51° to 64° F. during its development. At these temperatures the larval stage required from 4 to 5 weeks, and the pupal stage 4 to 5 days. Most larvae and pupae were attached to the downstream and under surfaces of small rocks but some were also on dead leaves and small twigs. Populations of immature stages did not reach great numbers at any of the study sites. These populations varied from approximately 25 to 150 per square foot in the different streams studied.

Next to *P. decemarticulatum*, it is probably the latest spring species of *Prosimulium* which occurs in the state. In one stream where it was found in association with members of the *P. hirtipes* complex, the larvae did not appear until the last larval population of the *hirtipes* complex had almost fully matured. First and second instars of *P. magnum* were first encountered in a small tributary of the Baraboo River in Sauk County on April 16, 1958. It was associated with members of the *P. hirtipes* complex, *P. gibsoni*, *C. mutata*, *S. corbis*, *S. tuberosum*, *S. venustum*, *E. gouldingi* and *E. latipes*, in various streams.

Eggs of *P. magnum* resist desiccation as they lie buried in the sand from late May or early June until the following March or April. There is one generation a year in Wisconsin.

Cnephia (*Cnephia*) *dacotensis* (Dyar and Shannon).—This is the most common and widespread species of *Cnephia* found in the state. Its immature stages occur in both permanent and temporary streams. In some small, temporary, meadow streams with muddy bottoms, populations were found to consist solely of *C. dacotensis*. Here the larvae and pupae were present in tremendous numbers. In one such area studied in Green Lake County, the bottom and sides of the stream were black with larvae and pupae, and all the vegetation trailing in the water was completely covered with the immature stages. This heavy population occurred all along a ½-mile stretch of the stream and may well have been present the entire length. Populations in such meadow streams may reach 10,000 to 20,000 or more per square foot.

Where they occurred in association with other species in larger rivers and streams, the populations of *C. dacotensis* were considerably fewer in number. Below lake outlets, where immature stages were found associated with *S. vittatum* and *S. decorum*, the populations were between 20 and 50 per square foot. Here they composed about one-eighth to one-fourth of the total populations. In other streams not originating from lake outlets, *C. dacotensis* populations were between 50 and 100 per square foot. Here these numbers comprised about 50% to 75% of the total populations.

Hatching of eggs in the spring depends on the water temperature of the river or stream in which the eggs are found. First-instar *C. dacotensis* larvae were present in streams shortly after the water temperature had reached 41° F. In Rock County (extreme south-central Wisconsin) both first- and second-instar larvae were present in Otter Creek on April 4, 1958, when the water temperature was 45° F. In Green Lake County (central Wisconsin) these early instars did not appear until April 12, 1958, at which time the water temperature was 47° F. Some second- and third-instar larvae were collected from Burnett County (extreme northwestern Wisconsin) on May 3, indicating a late April hatch. The water temperature on this date was 57° F. The larval stage required from 4 to 5 weeks with water temperatures rising from near 40° to 60° or 65° F., whereas the pupal stage was found to last from 5 to 7 days. The most common associates in streams not originating from lake outlets were *S. venustum*, *S. vittatum*, and *P. gibsoni*. *Cnephia mutata*, *E. aureum*, *E. gouldingi*, and *E. latipes* were less frequently associated.

This species has one generation a year, with the eggs remaining in a dormant state for 8 to 9 months. It has a wide range of tolerance for several different types of streams and consequently is an abundant and widespread species. It is not a pest species, however, because the adults are nonblood-sucking.

Cnephia (*Stegopterna*) *mutata* (Malloch).—*Cnephia mutata* occurs primarily in the northern counties, and is not common in the state. The immature stages were found most frequently in

small, temporary or permanent forest streams which usually had gravel bottoms. Larvae and pupae were attached to small stones, sticks, and occasionally trailing grasses. Their numbers usually made up only 2% to 5% of the total populations in such streams.

Duration of the larval and pupal stages was not determined. Stream collections indicate there is a single generation a year and that larvae hatching from overwintering eggs first appear in temporary streams in southern Wisconsin about the first week in April. However, in many young streams in the northern forest region, *C. mutata* was found to overwinter in the larval stage. Populations consisting of third to fifth instars were encountered in this area during the last week of March in both 1958 and 1959.

The most common associates of the species are members of the *P. hirtipes* complex, *S. venustum*, *E. pugetense*, and *E. latipes*. Occasionally it was found associated with *P. magnum*, *P. gibsoni*, *P. decemarticulatum*, *C. dacotensis*, and *S. tuberosum*.

Cnephia (*Ectemnia*) *taeniatifrons* (Enderlein).—This species is largely confined to the western counties bordering the Mississippi River. Adults have been collected only near the largest rivers of the state such as the Mississippi, Wisconsin, and St. Croix. A record from the Oconto River in Shawano County has proved the only exception to this relationship between the largest rivers in the state and species distribution.

Cnephia taeniatifrons is the earliest species of black fly found in Wisconsin. It overwinters in the larval stage and the first mature larval populations were encountered during the last week in March and the first weeks of April in 1959. In the Oconto River at Pulcifer, Wisconsin, the immature stages were found in extremely fast-flowing areas where the river width was approximately 30 yards. Collections could only be made about 10 feet out from the banks as the current velocity farther out in the river was too swift to permit one to stand. The immature stages were found at depths of 6 inches near the banks up to depths of 3 feet about 10 feet out. Both stages were found attached only to large rocks. All larvae at this collection site were attached to the exposed undersurfaces of rocks. Most of the pupae, however, were attached to the upper surfaces and sides of the rocks.

The pupae were encased in cocoons about halfway out on stalks composed of diatoms, sand, and detritus. These stalks were 8 to 15 millimeters long and their bases were attached to rocks by a circular or ellipsoidal mass of gummy material, presumably secreted by the salivary glands of the larvae. These stalks were similar to those described by Stone and Jamnback (1955) for *C. loisae* Stone and Jamnback. The open end of the cocoon faced toward the apex of the stalk, with the pupal respiratory filaments partially exposed.

In the Oconto River the density of *C. taeniatifrons* was estimated at 5 per square foot of river area sampled, with the density increasing farther out from the banks. The densest larval aggregation was 20 individuals on the undersurface of a rock roughly 12 inches in diameter, and likewise the most pupae found on any one rock was 14.

In this river, where it was associated with members of the *P. hirtipes* complex, *Prosimulium* species #1, and *S. vittatum*, *C. taeniatifrons* comprised about 30% of the total population. The water temperature at the time maturing larval populations were found was 35° F. In 1959, emergence of adults was almost completed at this site on April 7, at which time the water temperature had risen to 41° F.

Although adults were much more common along the Mississippi and Wisconsin Rivers, the immature populations were more difficult to find in these large rivers. This was due largely to deeper water and annual spring floods. By the time these rivers had receded into their normal channels, emergence of adults was usually complete.

On April 18, 1959, sparse populations of larvae and pupae were found attached to trailing vegetation and scattered rocks along the banks of the Wisconsin River in Crawford County. These *C. taeniatifrons* populations consisted largely of pupae and were associated with *Prosimulium* species #2, *E. johannseni* and *S. vittatum*. However, this population may have been washed into an unnatural habitat by the extensive spring flooding. In these situations the larvae of *taeniatifrons* were all attached within an inch or two of the river bottom at depths of 2 to 3 feet whereas the stalked pupae were all found near the water surface. The water temperature was 52° F.

Although many adults emerged on April 19 and 20 from pupae collected on April 18, no adults were observed in the field while collections were being obtained. Adult collection records from previous years indicate a single generation a year.

Eusimulium aureum (Fries).—*Eusimulium aureum* has a spotty statewide distribution, but is relatively common in some areas of northern Wisconsin. The larvae and pupae occurred in the smaller, rocky streams whose current velocities usually did not exceed 3 feet per second. Common substrata were rocks or trailing grasses. The immature stages frequently comprised about 2% to 10% of the total populations in various streams. In spite of its small numbers in individual streams, *E. aureum* was fairly common in collections because of the many streams in which it occurred. This is a late spring species, and larvae did not appear in streams until the water temperature warmed up to about 52° F. Immature stages have been collected in temperature ranges of 52° to 70° F. They are not generally found in the colder streams of the state.

The two most commonly associated species

were *S. venustum* and *S. tuberosum*. Less frequent associates were *S. vittatum*, *S. decorum*, and *C. dacotensis*. *Eusimulium aureum* has at least two generations a year in the state. In 1958, first-generation larvae hatched during the last weeks in May and pupae were first encountered between middle and late June. In 1957 and 1958 members of the second and possibly third generations were present during July and August. Occasional specimens were collected until mid-September. This species overwinters in the egg stage.

Eusimulium croxtoni (Nicholson and Mickel).—At the present time *E. croxtoni* is known only from Wood County in Wisconsin. However, as it is found in Minnesota and Canada (Nicholson and Mickel 1950; Fallis et al. 1956), it probably occurs throughout all the forest regions of central and northern Wisconsin.

The immature stages have been found in temporary drainage creeks and in young streams flowing through wooded areas. In young streams, the *E. croxtoni* populations consisted only of pupae on June 16, 1959. The water temperature at this time was 64° F. Because emergence of adults was almost completed and many empty cocoons were damaged or washed away, it was not determined what percentage of the total population *E. croxtoni* comprised. All pupae were found attached to small rocks in a current velocity of about 2 feet per second. Associated species in the young streams were *S. decorum* and *S. venustum*.

In a small, temporary forest creek *E. croxtoni* was found associated with *S. venustum*, where it comprised 60% of a population numbering approximately 20 larvae and pupae per square foot of stream bed area. The immature stages were found on tiny rocks and grass in about equal numbers. They were attached to the undersides of grass blades or to the sides and exposed undersurfaces of rocks. The current velocity here was approximately 0.5 feet per second. On July 16, 1959, the population of *E. croxtoni* consisted of 14% pupae, 59% mature larvae, and 27% immature larvae. The water temperature was 60° F.

The time required for larval and pupal development was not determined. In the laboratory, adults emerged from dark pupae within 2 to 4 days after collection. There is apparently a single generation of this species in the state.

Eusimulium gouldingi (Stone).—Although this species has a statewide distribution, it occurs in the greatest numbers throughout northern Wisconsin. It has been collected only from temporary streams, and is most abundant in small, rocky, forest streams. During the first week of May in both 1958 and 1959, maturing larval populations and pupae were collected at water temperatures ranging from 50° to 59° F. The immature stages were generally found in current velocities of less than 3 feet per second.

Larvae and pupae ranged from 5 to 60 per square foot of selected substrata in various streams and comprised 5% to 20% of the total immature populations. Rocks were the most common attachment sites, but in a few streams larvae were also found on grasses. Pupae were attached to the exposed undersurfaces of small rocks. The duration of the larval stage was not determined. Pupae collected from streams and held in the laboratory on moist cotton pads required 3 to 4 days to mature.

Eusimulium gouldingi was found associated with the following species: *P. gibsoni*, *P. decemarticulatum*, *P. magnum*, *C. dacotensis*, *S. venustum*, and *E. latipes*. The species has a single generation a year in Wisconsin.

Eusimulium johannseni (Hart).—This species appears to be confined to the southern agricultural region of the state. Its immature stages have been collected only from the Wisconsin River in Crawford County, but adults have been taken in several other counties. On April 18, 1959, larvae and pupae were found attached to aquatic vegetation near the banks of the Wisconsin River. They were found at depths of 4 to 18 inches where the current velocity was 1 to 2 feet per second. At this time, the river had almost receded into its normal channel following extensive spring flooding. The water temperature was 52° F.

Eusimulium johannseni comprised approximately 50% of the total black fly populations where they were collected in association with *Prosimulium* species #2, *C. taeniatifrons*, and *S. vittatum*. By April 18, the majority of *E. johannseni* larvae were mature and two pupae were found. The longevity of the immature stages was not determined, but early spring river collections indicate that this species may overwinter in the larval stage. From the immature and adult collection records, it was determined that the species has a single generation a year. In 1958, adults were first collected on April 20.

Eusimulium latipes (Meigen).—*Eusimulium latipes* is largely restricted to northern forest regions of the state. Its larvae and pupae have been collected only from small, rocky, semipermanent streams in heavily wooded areas. Water temperatures of these tiny streams ranged from 44° to 61° F. during larval and pupal development. Current velocities of various streams ranged from 1 to 3 feet per second. In 1957 and 1958, these streams became dry in late May or early June and remained dry until the following spring.

The larval stage required about 1 month and the pupal stage lasted approximately 1 week. The populations of *E. latipes* did not exceed five per square foot and usually were much less. Consequently they constituted a very small portion of total stream populations. Common associates in the temporary streams were *P. magnum*, *P. gibsoni*, *C. mutata*, and *S. venustum*. Occasion-

ally it was found associated with *C. dacotensis* and *E. gouldingi*. There is one generation a year, with the summer, fall, and winter being passed in the egg stage.

Eusimulium pugetense (Dyar and Shannon).—Collection records to date indicate that *E. pugetense* is restricted to the northern forest regions of the state. This is one of the earliest spring species of the genus *Eusimulium*. It is generally restricted to smaller, relatively cold, forest streams with sand and gravel bottoms, although it has also been collected from larger rivers such as the Oconto and Pelican while they are at spring flood stage.

Larvae and pupae were almost always collected from vegetation trailing in the current. Early spring stream investigations indicate that *E. pugetense* larvae probably first appear in early March. Second- and third-instar larvae were found together with *C. mutata* in a number of streams during late March. The first pupae were observed on May 10, 1958, in Marinette and Oneida Counties. At this time, the smaller, colder streams (42° F.) had populations that consisted primarily of larvae. In one such stream, the ratio was 35 larvae to each pupa. Warmer rivers (50° to 54° F.), on the other hand, contained only pupal populations, and about half of the adults had emerged.

This species was found to be locally common in only one small forest stream in northern Marinette County. Here it comprised 90% of the total larval and pupal population which was estimated at 10 per square foot of selected substrata. In other streams and rivers, it was relatively rare, making up about 1% to 5% of the total populations.

The most commonly associated larvae in the larger rivers were *S. vittatum* and *S. jenningsi*. *Cnephia mutata*, *S. venustum*, and sometimes members of the *P. hirtipes* complex were found associated with the immature stages in smaller forest streams. From collection records of the immature stages, it appears that *E. pugetense* has a single generation a year.

Simulium (*Gnus*) *corbis* Twinn.—*Simulium corbis* is restricted to the northern forested areas of the state. It was collected most frequently in small, cold streams flowing through swampy forest areas. Such streams were about 2 to 5 feet wide, 6 to 18 inches deep, and had water temperatures between 42° and 50° F. Larvae were almost always found attached to rocks. In warmer streams (above 50° F.) about 10% of the larvae were mature on May 10, 1958, but the populations in colder streams were composed only of early instars on this date.

In various streams, *S. corbis* made up from 20% to 50% of the total populations, which ranged from 75 to 150 larvae per square foot. Their numbers were greatest in the smaller streams where the largest populations consisted of 30 to 60 larvae per square foot. In Wisconsin, the larval stage apparently requires about 5 to 6 weeks. Pupal maturity required at least 8 days. Sommerman et al. (1955) reported 3 to 5 weeks for larval development and about 10 days for the pupae to mature in Alaskan streams at water temperatures from 50° to 60° F.

S. corbis overwinters in the egg stage and there apparently is but a single generation a year in Wisconsin streams. Associated species were members of the *P. hirtipes* complex, *P. magnum*, *S. tuberosum*, and *S. venustum*

Simulium (*Byssodon*) *meridionale* Riley.—To date this species has been found only in the southern and southwestern areas of the state, where its immature stages occur in the Mississippi and Wisconsin Rivers. Adults have been collected up to 15 miles from the known breeding sites.

Although adult flies were collected in late May and early June, the immature stages were not found until about mid-June. The larvae and pupae occurring in the rivers at this time probably belong to the second generation.

Larvae and pupae were most commonly attached to the sides of small rocks or to the undersurfaces of grass blades at water depths of 2 to 6 inches, but usually only on vegetation in deeper water. Most individuals were found only an inch or two below the water surface, and larvae and pupae were rarely encountered at depths greater than 6 inches below the water surface. Current velocities at these sites were usually less than a foot per second. The temperature of the water varied from 68° to 76° F.

It requires about 3 weeks for the larvae to mature whereas the pupae mature in 3 to 4 days. There are at least four generations each year and adults can be collected as late as October. In different sections of the rivers, these populations were either associated with *S. vittatum* or consisted solely of *S. meridionale*. *Simulium meridionale* probably overwinters in the egg stage in this area.

Simulium (*Byssodon*) *rugglesi* Nicholson and Mickel.—*Simulium rugglesi* has been found only in central and northern Wisconsin. Information on the biology of the immature stages is largely lacking. Its larval and pupal stages have not as yet been associated. *Simulium rugglesi* is apparently a late spring and summer species, as pupae have been encountered only in mid-July. It has been found in young rivers and in the larger types of young streams. The pupae were always attached to the upper surfaces of aquatic vegetation from 1 to 4 inches beneath the water surface. Current velocities ranged from 1 to 2.5 feet per second while water temperatures varied from 57° to 66° F.

In the young streams, *S. rugglesi* was found associated with *S. tuberosum* and *S. venustum*, and in the young rivers the associated species were *S. venustum*, *S. jenningsi* and *S. luggeri*. In the

young streams it comprised 4% of the total populations that were between 25 and 50 larvae per square foot. In the young rivers *S. rugglesi* made up only 2% of the total black fly populations that consisted of approximately 500 larvae per square foot of selected substrata.

The number of generations a year and duration of the larval and pupal stages were not determined. The species probably passes the winter in the egg stage.

Simulium (*Simulium*) *decorum* Walker.—*Simulium decorum* is statewide in distribution, but its habitat is usually restricted to those areas of rivers and streams just below lake outlets or short distances below dams that contain large bodies of water. The immature stages were commonly found in current velocities of 3 to 4 feet per second. The water temperature in these areas was usually warm (58° to 69° F.). First-generation larvae require approximately 4 weeks to mature and the second generation about 3 weeks. The pupal stage requires about 3 to 5 days.

The immature populations occasionally reach tremendous numbers. These numbers occur most often where homogeneous populations are found on the downstream side of rocky dams and on beaver dams. From 1,000 to 2,000 larvae and pupae may be found per square foot. Below lake outlets, where they are often associated with *S. vittatum*, they generally comprise about 50% of the total populations which have been found to vary between 50 and 500 larvae and pupae per square foot. The most commonly associated species in warmer water is *S. vittatum*, but *S. venustum* and *C. dacotensis* are also frequent associates. *E. croxtoni* was found associated less frequently.

This species has several generations a year in Wisconsin. Depending on stream conditions, the first generation usually occurs between mid-May and mid-June, and the succeeding generations may be present until September. It passes the winter in the egg stage.

Simulium (*Simulium*) *jenningsi* Malloch.—Although this species has a statewide distribution it is most common throughout the northern and central areas of the state. The immature stages are restricted to the young river type of flowing water in these areas. Within the rivers themselves, the habitat is further restricted to clear, shallow, rocky, swift portions. Larvae have not been collected in muddy rivers or in deeper, slow moving areas of relatively clear rivers. The larvae and pupae were most commonly found attached to downstream and under sides of rocks in small rapids, but they were also found on various types of aquatic vegetation in certain rivers.

Populations ranged from 200 to 1500 or more per square foot in the rapids of rocky rivers, but where vegetation served as the substratum, the densest populations found were about 800 to 900 larvae and pupae per square foot of selected substratum. Larvae and pupae were normally found at depths of 1 to 6 inches on vegetation but occasionally were found as deep as 18 inches on some rocks. The water temperature of rivers where *S. jenningsi* was found ranged from 55° to 72° F. during its development. There are several generations a year, and adults of the first generation are usually on the wing by the third week in May. First generation larvae require about 5 to 6 weeks to mature and the pupae 5 to 7 days. In warmer water the second generation is more rapid.

The two species most commonly associated with *S. jenningsi* in Wisconsin rivers are *S. venustum* and *S. luggeri; S. vittatum* is found less often. This species overwinters in the egg stage.

Simulium (*Simulium*) *luggeri* Nicholson and Mickel.—This species closely resembles *S. jenningsi* both in morphology and biology, and the immature stages are frequently found together. However, *S. luggeri* has been found only in the central and northern regions of the state. The general habitat descriptions and ecological relationships are largely the same as for *jenningsi*. There are at least two generations a year in Wisconsin, and, like *S. jenningsi*, the winter is passed in the egg stage.

Simulium (*Simulium*) *venustum* complex.—In treating the following three species as a group or complex, I am following the temporary treatment of this group adopted by Stone and Jamnback (1955). These authors stated that "The three species *Simulium tuberosum* (Lundstr.), *S. venustum* Say, and *S. verecundum*, n. sp., form a very closely related group, scarcely distinguishable in the pupa, female, or the male except for the genitalia."

The larvae of *S. tuberosum* are easily distinguished from both *S. venustum* and *S. verecundum*, but the latter two species can be separated only if living or freshly killed specimens are available. The bodies of *S. venustum* larvae are characterized by having a reddish color while those of *S. verecundum* have white bodies. All three species are members of the subgenus *Simulium*.

The complex appears to be statewide in distribution. Immature stages were found in all types of smaller permanent streams. They were also found occasionally in some of the semipermanent streams, and more frequently in the larger rivers and streams. As a group these three species are as common as or possibly more common than *S. vittatum*.

Like *S. vittatum*, they were sometimes found in tremendous numbers in favorable streams, i.e., those with few parasites and predators, abundant food, warm water, and adequate substrata. They were frequently parasitized by nematodes and sometimes by sporozoans. Usually only a small percentage of the total populations were parasitized but occasionally 50% or 60% of a population was found infested with nematodes.

Simulium tuberosum and *S. venustum* have three or more generations a year in Wisconsin, whereas *S. verecundum* probably has at the least two generations in most areas of the state where it occurs. *Simulium tuberosum* and *S. venustum* first appeared in streams during early April in southern Wisconsin, but not until 2 to 4 weeks later in most northern streams. *Simulium verecundum* occurred later. The immature stages were found from July to September.

Simulium venustum larvae hatching from overwintering eggs in small forest streams developed more rapidly than did associated populations of *E. pugetense* which had probably hatched in late February or early March. Although larvae of *E. pugetense* were present in these streams at least a month before the appearance of *S. venustum* larvae in mid-April, both species were beginning to pupate by May 10, and the adults of both species were flying at approximately the same time.

These three species were commonly found associated with one another (especially *venustum* and *verecundum*) and often with populations of *C. dacotensis*, *S. decorum*, *S. jenningsi*, and *S. vittatum*. *Simulium venustum* was less frequently found associated with *P. decemarticulatum*, *P. gibsoni*, members of the *P. hirtipes* complex, *P. magnum*, *C. mutata*, *E. aureum*, *E. croxtoni*, *E. gouldingi*, *E. latipes*, *E. pugetense*, *S. corbis*, and *S. rugglesi*; whereas *S. tuberosum* was occasionally found with populations of *P. magnum*, *C. mutata*, *E. aureum*, *S. corbis*, and *S. rugglesi*. All three species pass the winter in the egg stage.

Simulium (*Neosimulium*) *vittatum* Zetterstedt.—This is the most abundant and widespread species of black fly in the state. The immature stages show a wide range of tolerance for almost any type of flowing water. They are found in bodies of water ranging from tiny meadow streams to the larger rivers of the state, and varying in turbidities from muddy to crystal clear. The immature stages are especially common in the young and old stream types of flowing water. In streams having abundant vegetation, populations were often encountered which numbered 2,000 to 4,000 larvae and pupae per square foot. The immature stages were found attached to rocks, submerged branches, leaves, and cans, among other things; but vegetation trailing in water was the preferred substratum.

Simulium vittatum has two different methods of overwintering in permanent flowing water. It is capable of passing through the late fall and winter in either the egg or larval stage. Both methods of overwintering are sometimes found in the same stream, and the overwintering stage in given streams may vary from one year to another.

In 1957–1958, large populations of overwintering larvae were present in streams of southern Wisconsin (south of 45° north latitude). Collections obtained from streams in this area in February and early March consisted largely of third- and fourth-instar individuals. However, in this same year the species overwintered as eggs in the region of the state north of 45° north latitude. These *S. vittatum* populations hatching from overwintering eggs in northern streams were first detected in early March. Investigations of the same streams in December and February revealed no black fly larvae present. During March 1958 the populations overwintering as larvae in other areas of the state had not yet pupated. It was thus established that the newly hatched populations occurring in the northern streams were not second generations produced by earlier generations which might have passed through the winter in the larval stage.

During 1958–1959, this overwintering pattern was not as clearly marked between the northern and southern areas of the state as it had been in 1957–1958. On December 23, 1958, a small population of overwintering second-instar larvae was found in one of the northern streams in which the species had overwintered only as eggs in 1957–1958. However, as in 1958, a population hatching from overwintering eggs also appeared in this stream in March of 1959. This confusing overwintering picture was more noticeable in the southern half of the state in 1958–1959. Here, approximately 20 of the streams which had contained large populations of overwintering larvae in 1957–1958, were found to contain only sparse populations of overwintering larvae in March 1959. On March 6 and 7, these sparse populations of overwintering larvae were found to be accompanied by large populations of newly hatched larvae. Also, some of the streams in which overwintering larval populations were present in March 1958 contained only populations that had overwintered as eggs in 1959.

One of the streams (Black Earth Creek) that had a large overwintering larval population in February and March, 1958, also contained a large overwintering larval population in February and March, 1959. In this stream there was no evidence of a separate population which had overwintered as eggs.

Two possible explanations for these different methods of overwintering for *S. vittatum* are: (1) the species in Wisconsin may consist of two distinct subspecies or species that differ biologically from one another (especially in the method of overwintering), or (2) the overwintering stage is inherently controlled by the last generation of ovipositing females in the fall in response to some external stimuli.

The duration of the larval and pupal stages is influenced by the temperature of the water and the available food supply. In 1957–1958, the overwintering larval populations in southern Wisconsin required about 6 months to mature

when water temperatures were between 32.5° and 41° F. An occasional pupa was collected as early as mid-February. The pupae require about 1 or 2 weeks to mature at the above temperatures.

In northern areas of the state where the winter was passed in the egg stage in 1957–1958, larvae first appeared in early March when water temperatures varied from 33° to 35° F. in different streams. Some members of these populations were mature by the last week in April. For instance, in Turtle Lake Creek in Barron County a small population consisting of second- and third-instar larvae which had recently hatched from overwintering eggs was first encountered on March 15, 1958. At this time the water temperature was 34.5° F. The first maturing members of this population began pupating early in the last week of April. A number of first generation females were observed ovipositing in this stream on May 3 and 4, at which time 95% of the first generation had pupated. A sparse population of the second generation early instar larvae was present on these dates along with a large population of newly hatched first-generation *S. venustum*. At this time the water temperature had risen to 52° F. Thus, at water temperatures warming from slightly above freezing to the low fifties, the first generation of *S. vittatum* required about 8 to 9 weeks to develop from newly hatching first-instar larvae to adults.

During the warm summer months when water temperature was above 60° F. in most streams this species inhabited, the larval stage lasted for approximately 3 weeks whereas the pupal stage generally lasted 3 to 4 days.

Simulium vittatum may have four to five generations a year in different areas of Wisconsin. The exact number of generations was difficult to determine because of ovipositing females dispersing into the study areas as the summer progressed. This resulted in several overlapping generations, with larvae of all stages present in many streams throughout the spring, summer, and fall. The most commonly associated species throughout the state are *S. decorum*, *S. tuberosum*, and *S. venustum*. Other species occasionally found with *S. vittatum* are members of the *P. hirtipes* complex, *C. dacotensis*, *C. taeniatifrons*, *E. aureum*, *E. johannseni*, *E. pugetense*, *S. jenningsi*, *S. rugglesi* and *S. meridionale*.

Probably because of its wide occurrence, this species was found parasitized more frequently than any other. The most common parasite of the larvae is a mermithoid nematode, but specimens were also parasitized by microsporidian protozoans. The parasitized populations infested with nematodes were more frequently found in smaller, muddy-type streams where the percentage of the parasitized populations sometimes reached 90%.

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BIOLOGICAL NOTES ON PACIFIC COAST APHID PARASITES, AND LISTS OF CALIFORNIA PARASITES (APHIDIINAE) AND THEIR APHID HOSTS (HYMENOPTERA: BRACONIDAE)[1]

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ABSTRACT

Biological notes on distribution, new rearing data, hyperparasites, diapause, and other observations are given for 18 California species and 5 British Columbia species of Aphidiinae, based on scrutiny of 1500 specimens reared from 1956 to 1958. In addition, distribution, hosts, and diapause are noted for 9 species of secondary parasites. There are now 26 described species of Aphidiinae known from California, 18 of which occur in southern California. These parasites attack 68 species of aphids in 24 genera, of which 23 species and 4 genera are added as new hosts. Parasite-host and host-parasite lists are added for easy reference. New records for California aphid parasites are *Aphidius* (*Aphidius*) *nigripes* Ashmead, *A.* (*A.*) *pisivorus* Smith, *A.* (*Lysiphlebus*) *chrysoaphidis* Smith, and *Praon unicus* Smith. *Asaphes fletcheri* (Crawford), a primary parasite of *Aphidius* (*A.*) *nigriteleus* Smith, is also a new California record. New records for British Columbia aphid parasites are *Aphidius* (*Aphidius*) *ohioensis* Smith, *A.* (*A.*) *pisivorus* Smith, *A.* (*A.*) *ribis* Haliday and *Ephedrus californicus* Baker. *Euneura lachni* (Ashmead), a primary parasite of *Aphidius* (*Protaphidius*) *ponderosae* Muesebeck, is also a new British Columbia record.

In July 1956, in conjunction with a project on the biological control of the spotted alfalfa aphid, *Therioaphis maculata* (Buckton), we began accumulating notes on various aphid parasites and hyperparasites relating primarily to southern California fauna. Our main objectives were to determine (1) what aphid parasites occur in California, (2) to what extent these parasites aid in controlling aphid populations, (3) what aphid species are attacked, (4) what hyperparasites are involved, (5) to what extent these hyperparasites hinder the effectiveness of the primary parasites, and (6) other biological data.

This is the first of a planned series of articles on aphid parasites. Two wasp genera (*Aphelinus* Dalman and *Encarsia* Foerster) of the family Eulophidae, subfamily Aphelininae, known to be internal parasites of aphids have been omitted from this study. Several host-parasite records of *Aphelinus* in North America are known, but to our knowledge the only *Encarsia* species to have been recorded as an aphid parasite was one from a sugarcane aphid in Java (Hazelhoff 1929).

METHODS

All samples were collected in the field, brought into the laboratory, and reared in cylindrical half-pint ice-cream cartons, each covered with a petri dish. Laboratory temperatures ranged from 70° to 80° F., and relative humidities ranged from 50% to 70%. As soon as any secondary parasite emerged it was removed to preclude any hyperparasitism in the container. Adult primary parasites were allowed to die normally in order to avoid obtaining teneral specimens. Specimens resulting from these experiments were deposited either in the U. S. National Museum collection, Washington, D. C., or in the collection of the Department of Biological Control of the University of California, Riverside.

The works of Gahan (1911), Smith (1944), Muesebeck et al. (1951), Thompson (1953), MacGillivray and Spicer (1953), Shands et al. (1955), and Krombein et al. (1958) have been

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consulted for known aphid-parasite associations and distributions in North America. The principal reference sources for aphid terminology and relationships used here were those of Swain (1919), Baker (1920), Hottes and Frison (1931), Patch (1938), and Palmer (1952).

The data recorded under each of the species listed are new except as noted. Parasite synonymies have been omitted, since complete synonymies of the parasites have been given by Smith (1944) and by Muesebeck et al. (1951). Citations are given for three species not listed in these references.

For this study over 1500 primary parasites (Aphidiinae) were collected and reared from July 1956 to December 1958. These represented 18 California species. In addition, another 150 individuals, representing 5 species, were reared from aphids collected in British Columbia in June 1957. Of the 15 species previously recorded from California (south of the Tehachapi Mountains) we have recovered 12 and have found 3 additional species not previously known to occur here. Altogether, 26 described species are now known from California, and of these 18 are in southern California. These parasites are known to attack 68 species of aphids in 24 genera, of which 23 species of 4 genera are cited as new hosts at this time.

Over 250 secondary parasites were also reared with the Aphidiinae. These represented the following species: *Asaphes californicus* Girault, *A. fletcheri* (Crawford), *Euneura lachni* (Ashmead), *Coruna clavata* (Walker), *Pachyneuron siphonophorae* (Ashmead) [all Pteromalidae]; *Aphidencyrtus aphidivorus* (Mayr) [Encyrtidae]; two species of *Alloxysta* Foerster, seven species of *Charips* Marshall [all Cynipidae]; and a species of *Lygocerus* Foerster [Ceraphronidae]. *P. siphonophorae*, *A. californicus*, and the *Charips* species were by far the most commonly reared species.

For the convenience of the reader, parasite-host and host-parasite lists are included in this paper. Recorded hosts are given along with the primary parasites and, usually, the first author to associate the host species. New hosts are given under a separate heading. The form of this list is similar to that published by MacGillivray and Spicer (1953). It is recommended that other workers prepare similar lists when publishing studies on parasite-host relationships.

BIOLOGICAL NOTES

Aphidius (Aphidius) alius Muesebeck

Aphidius (Aphidius) alius Muesebeck 1958, Ent. News, 69: 142, fig. 2.

Distribution.—Known only from central and southern California.

New Rearing Data.—The type series was described from several specimens reared from *Macrosiphum rosae* (L.) on *Rosa* sp. at Riverside, California. Other rearings from the same aphid on rose were from Wheeler Ridge, Kern County, April 24, 1958, and Reedley, Fresno County, December 26, 1957.

Hyperparasites.—About 50% of the cocoons brought to the laboratory were hyperparasitized. Most of these parasites were *Pachyneuron siphonophorae* (Ashmead), but *Asaphes californicus* Girault, several *Charips* spp., and one large *Lygocerus* sp. also were reared.

Diapause.—A preliminary discussion of the diapause situation in *A. alius* was given by Schlinger (1960). Approximately 90% of the remaining unhyperparasitized cocoons collected at Riverside, California, during March and April, 1958, were in diapause. Dissections of the March population in June revealed live diapause larvae and live *Charips* larvae. Two females of a *Charips* sp. emerged from the diapause specimens which had been in the laboratory for 5 months. However, none of the diapause individuals of *A. alius* emerged, and after 1 year had elapsed, dissections of the remaining cocoons revealed only dead larvae and a few dead pupae.

Observations.—*Aphidius alius* is not a common parasite, at least not on its only known host, *Macrosiphum rosae* (L.). This is probably due to the high degree of diapause and to heavy hyperparasitization as well as nonsynchronization of the host and parasite. Perhaps on another host, *A. alius* will be found to be more common.

Aphidius (Aphidius) confusus Ashmead

Distribution.—California and Arizona (Muesebeck et al., 1951).

New Rearing Data.—About 20 individuals were reared from aphids at the following localities: Riverside, March 24 and April 13, 1958, from *Macrosiphum rosae* (L.) on *Rosa* sp., and July 28, 1958 from *Macrosiphum* sp. on *Artemisia dracunculoides* L.; Pedley, July 5, 1958, from *Macrosiphum rudbeckiae* (Fitch) on *Calendula officinalis* L.

Hyperparasites.—Only one specimen of *Pachyneuron siphonophorae* (Ashmead) was reared from this species at Riverside.

Diapause.—Several individuals were obtained from both *Macrosiphum rosae* (L.) and *M. rudbeckiae* (Fitch) which were in complete diapause. The diapause condition in *Aphidius confusus* was discussed by Schlinger (1960) on its host *M. rosae*.

Observations.—*Aphidius confusus* does not appear to be a common species in southern California, at least on the hosts named above. We have only reared this species on four different occasions. It appears to be restricted to hosts of the genus *Macrosiphum*, and perhaps it will be found to be more common on another species of this genus at a later date.

Aphidius (Aphidius) nigripes Ashmead

Distribution.—Connecticut to Maryland; Ohio (Muesebeck et al. 1951); New Brunswick (MacGillivray and Spicer 1953); Maine (Shands et al. 1955); North Carolina, Michigan, Kansas, Minnesota (Krombein et al. 1958), and California (NEW RECORD).

New Rearing Data.—About 30 males and females were reared from *Macrosiphum rosae* (L.) on *Rosa* sp. at Riverside, California, during March and April 1958.

Hyperparasites.—*Asaphes californicus* Girault and a *Charips* sp. were reared from nondiapause cocoons. *Charips* sp. were also reared from diapause cocoons which had been in the laboratory for over a 6 months' period.

Diapause.—The diapause condition in *Aphidius nigripes* was reported by Schlinger (1960) and is about the same as that noted in *A. alius*.

Observations.—The rearings reported above are first record of *Aphidius nigripes* west of the Rocky Mountains and the first true record of *Macrosiphum rosae* as one of its hosts. This species is about as common as *Aphidius alius* in Riverside. It parasitizes mostly species of *Macrosiphum*; however, *Aphis abbreviata* Patch is listed as a host by MacGillivray and Spicer (1953).

Aphidius (Aphidius) nigriteleus Smith

Distribution.—Connecticut, Indiana, Massachusetts, Michigan, Ohio, and Oregon (Muesebeck et al. 1951); New Brunswick (MacGillivray and Spicer 1953); Maine (Shands et al. 1955); California, Maryland, Washington, D. C., and Washington (Krombein et al. 1958).

New Rearing Data.—About 150 individuals have been reared from hosts found in the following California localities: Glendale, April 15, 1957, from *Aphis helianthi* Mon. on *Pittosporum tobira* Ait.; Riverside, March 12, 1957, from *Aphis rumicis* L. on *Rumex crispus* L.; Riverside, March 3, 1957, from *Phorodon menthae* (Buck.) on *Mentha arvensis* L.; Riverside, January 21 and March 27, 1958, from *Myzus persicae* (Sulz.) on *Viburnum suspensum* Lindl.; Bakersfield, May 21, 1958, from *Myzus persicae* (Sulz.) on *Carthamus tinctorius* L.; Riverside, February 21, 1958, from *Macrosiphum rudbeckiae* (Fitch) on *Calendula officinalis* L.

Hyperparasites.—*Asaphes fletcheri* (Crawford) was the only hyperparasite reared; this apparently represents a new record for California.

Diapause.—Not apparent at the time our samples were taken and reared.

Observations.—This widespread North American species is now known to attack 13 species of aphids in 7 different genera. Our rearings in southern California indicate that it is one of the more common parasites of *Myzus persicae* and that it rarely attacks *Macrosiphum rudbeckiae*. It is possible that *Aphidius nigriteleus* is not well adapted to any of the aphid species encountered so far in southern California.

Aphidius (Aphidius) ohioensis Smith

Distribution.—Arizona, Arkansas, Ohio, Tennessee (Muesebeck et al. 1951); New Brunswick (MacGillivray and Spicer 1953); Maine (Shands et al. 1955); Kansas (Krombein et al. 1958), and British Columbia (NEW RECORD).

New Rearing Data.—Ten males and females were reared from aphids collected at Skihist Camp, nr. Lytton, British Columbia, Canada, on June 2, 1957, from *Macrosiphum ambrosiae* (Thomas) on *Baccharis* sp.

Hyperparasites.—Unknown.

Diapause.—No diapause specimens were noted from the British Columbia individuals.

Observations. Only one population of this parasite was encountered on *Macrosiphum ambrosiae* in British Columbia.

Aphidius (Aphidius) pisivorus Smith

Distribution.—Idaho, Nevada, Ohio, Oregon, Utah, Virginia, Washington, D. C. (Muesebeck et al. 1951); New Brunswick (MacGillivray and Spicer 1953); Maine (Shands et al. 1955); California and British Columbia (NEW RECORDS).

New Rearing Data.—Numerous specimens have been reared from *Macrosiphum pisi* (Harris) on *Medicago sativa* L. from Cawelo, Kern County, California, during June-July and September-November 1956–58. Others were reared from the same host at Famosa, Kern County, California, in July 1957, and a few from Lancaster, Los Angeles County, in May 1957. Over 100 males and females were reared from *Macrosiphum albifrons* Essig on *Lupinus* sp. at Oxnard, California, on August 5, 1958. Seven males and females were reared from *Macrosiphum* sp. (not *pisi* or *rosae*) on *Rosa* sp., at Skihist Camp, nr. Lytton, British Columbia, on June 2, 1957.

Hyperparasites.—*Pachyneuron siphonophorae* (Ashmead), *Lygocerus* sp., and several *Charips* spp. were reared from the California series.

Diapause.—In November 1957, rearings from Cawelo, California, revealed that many of the *Aphidius pisivorus* individuals on *Macrosiphum pisi* were in diapause. A certain number of the larvae remained alive in diapause in the laboratory until July 1958. Dissections made in August 1958, however, showed that all had died in the interim period.

Observations.—*Aphidius pisivorus* is the only species of *Aphidius* reared from the pea aphid in the San Joaquin Valley, California. It occurs north of this valley, but to our knowledge does not occur south of Los Angeles County. In the San Joaquin Valley the parasite exhibits two distinct population peaks—one in late spring and one in late fall, both corresponding quite well with pea-aphid populations in the area. It does

not appear to be well adapted to the California pea aphid, for only on rare occasions has it been observed to be "common." However, along the coast of California *A. pisivorus* parasitizes *Macrosiphum albifrons* and has been reared in great numbers and in a good parasite-host ratio, so that it appears to be somewhat better adapted to this host, at least in the coastal climate.

Of *Aphidius* species attacking *Macrosiphum pisi* in California *A. pisivorus* is the most common, and since *Aphidius* (*Lysiphlebus*) *testaceipes* does not attack *M. pisi* on alfalfa in California, it is of interest that D. W. Jones of the Insect Identification and Parasite Introduction Laboratory at Moorestown, New Jersey, reported (in conversation) that *A. testaceipes* was the most important parasite of *M. pisi* in New Jersey, and that to his knowledge *A. pisivorus* did not attack this aphid on alfalfa in that area. It seems likely that either the parasites or the aphids, or both, have developed strains which so far have eluded taxonomic analysis.

Aphidius (Aphidius) pterocommae Ashmead

Distribution.—California, Massachusetts, Ohio, Washington, D. C. (Muesebeck et al. 1951); New Brunswick (MacGillivray and Spicer 1953).

New Rearing Data.—Six males and females were reared from *Pterocomma bicolor* (Oestl.) on *Salix* sp. taken at Golden Lake, Fresno County, California, on August 19, 1956, elevation 11,000 ft.

Hyperparasites.—Unknown.

Diapause.—No diapause specimens were present in the above sample.

Aphidius (Aphidius) ribis Haliday

Distribution.—Ontario, Canada, to Washington, D. C., and west to Iowa and Utah (Muesebeck et al. 1951); New Brunswick (MacGillivray and Spicer 1953); Manitoba (Krombein et al. 1958), and British Columbia, Canada (NEW RECORD).

New Rearing Data.—Four males and females were reared from *Capitophorus ribis* (L.) on *Malva parviflora* L. from Vancouver, British Columbia, on June 4, 1957.

Hyperparasites.—Unknown.

Diapause.—Several individuals from the sample taken appeared to be in diapause, but the extent of the diapause is not known.

Observations.—The Vancouver sample (see above) represented one of many similar infestations of parasites seen in southern British Columbia in June 1957. This particular sample contained several hundred parasites, but most of the immature parasites, as well as the aphids, were apparently killed by the heat in transit to California. It should be noted here that similar samples of *Aphidius pisivorus* and *A. ohioensis* were not damaged by the heat during the same trip. This, and its distributional data, suggest that *A. ribis* may be a cool-climate species.

Aphidius ribis is one of the few species of *Aphidius* that have been reared by various persons and have remained specific to one host, namely, *Capitophorus ribis* (L.).

Aphidius (Protaphidius) ponderosae Muesebeck

Aphidius (*Protaphidius*) *ponderosae* Muesebeck 1958, Ent. News, 69: 141, fig. 1.

Distribution.—Known only from the type locality in British Columbia.

Hyperparasites.—Six individuals of *Euneura lachni* (Ashmead) were reared from the type series.

Diapause.—None of the specimens of the type sample were in diapause.

Observations.—The type series was reared from *Cinara* sp. nr. *glabra* (G. and P.), but very few live, mature aphids could be found, although more than 10 pine trees were examined carefully. This seemed to indicate that *A. ponderosae* was an effective parasite on this aphid at that time.

Aphidius (Lysiphlebus) chrysoaphidis Smith

Distribution.—Idaho and Utah (Smith 1944); California (NEW RECORD).

New Rearing Data.—Nearly 100 individuals of this species have been reared from various hosts in southern California as follows: 15 males and females from *Aphis lutescens* Monell on *Nerium oleander* L., at Riverside, California, December 14, 1956; 20 males and females from *Aphis* sp. on *Pittosporum rhombifolia* Cunn., at Riverside, March 10, 1957; 5 males and females from *Aphis gossypii* Glover on *Hibiscus rosa-sinensis* L., at Riverside, August 19, 1957; 35 males and females from *Aphis heraclella* Davis on *Foeniculum vulgare* (L.), at Del Mar, San Diego County, California, August 30, 1957; 5 males from *Aphis helianthi* Monell on *Pittosporum tobira* Ait., at Glendale, Los Angeles County, California, April 15, 1957; 10 males and females from *Aphis gossypii* Glover on *Cotyledon* sp., at Glendale, December 23, 1956; 1 female from *Aphis pseudohederae* Theob. on *Hedera helix* L. at Ontario, Los Angeles County, California, November 19, 1956; 1 female from *Aphis* sp. on *Gardenia* sp. at Ontario, January 27, 1957.

Hyperparasites.—*Pachyneuron siphonophorae* (Ashmead), *Asaphes californicus* Girault, and several *Charips* spp. were reared from the above samples.

Diapause.—Not evident in any of the reared samples.

Observations.—This seems to be a very important aphid parasite in southern California, at least on the hosts named above. All known hosts fall within the genus *Aphis*, and in this regard it should be noted that *Aphidius chrysoaphidis* has been observed to oviposit and develop to a late larval instar in *Aphis spiraecola* Patch but, like *A. testaceipes*, has never been reared successfully from this host. This is true from aphids collected on the several different host

plants and whether this unsuccessful development is due to the small size of the aphid, the physiological condition of the aphid, or some other factor is not known, but the aphid invariably dies and turns dark brown or black before the parasite larva appears ready to form its cocoon. At this time the parasite larva also dies. For a further discussion of this developmental relationship see the observations below on *Aphidius testaceipes*.

Aphidius (Lysiphlebus) testaceipes (Cresson)

DISTRIBUTION.—Throughout the United States and in Mexico (Muesebeck et al. 1951); New Brunswick (MacGillivray and Spicer 1953); southern Canada (Krombein et al 1958); introduced and established in Hawaii (Williams 1931); Brazil (?), East Africa (?), and Bermuda (Thompson 1953).

New Rearing Data.—Over 800 individuals of this species have been reared from aphid hosts on the following plants in southern California: *Aphis lutescens* Monell on *Nerium oleander* L.; *Aphis helianthi* Monell on *Pittosporum tobira* Ait.; *Aphis gossypii* Glover on *Hibiscus rosa-sinensis* L.; *Aphis rumicis* L. on *Rumex crispus* L.; *Aphis* sp. on *Pittosporum rhombifolia* Cunn., *Viburnum suspensum* Lindl., *Citrus sinensis* (L.) Osbeck, and *Encelia actoni* Elmer; *Aphis pseudohederae* Theob. on *Fatshedera lizei* Guill., and *Hedera helix* L.; *Macrosiphum ambrosiae* (Thomas) on *Encelia actoni* Elmer; *Myzus persicae* (Sulz.) on *Vinca minor* L. and *Achillea filipendulina* Lam., all from Riverside, California. In addition, many specimens were reared from *Rhopalosiphum maidis* (Fitch) on *Hordeum* sp. (Calexico, California), on *Zea mays* L. (Del Mar, California), as well as from *Aphis medicaginis* Koch on *Medicago sativa* L., in southern and central California, and on *Salsola kali* var. *tenuifolia* Mey. (Lancaster, California).

Hyperparasites.—Both *Asaphes californicus* Girault and *Pachyneuron siphonophorae* (Ashmead) were frequently reared. In addition, at least five species of *Charips* and a species of *Alloxysta* were reared. It is noteworthy that the rather common *Aphidencyrtus aphidivorus* (Mayr) was not reared, nor is there any known record of this association in the literature.

Diapause.—No diapause specimens appeared to be present in the above samples. However, hibernation was apparent in several of the winter collections from central California, and it is possible that a weak diapause condition may occur farther north in the United States and Canada.

Observations.—*Aphidius testaceipes* is probably the most common and most obvious aphid parasite in southern California. It certainly should be considered a potential aid to any natural-control program of pest aphids.

More biological data have been given for this species than for all other North American species combined, and due to its widely recorded host range and its great distribution, it has been considered by many workers to be the most effective parasite of aphids. The fact that no less than 18 specific names have been applied to *Aphidius testaceipes* since its original description (see Muesebeck et al. 1951) clearly illustrates the degree of variation (both morphological and host-influenced) that exists with this species. The present authors tend to agree with Smith (1944, p. 83) who proposed that some of the synonyms may be revived after more extensive biological work is completed with respect to hosts, aphid host plants, and parasite distributions.

On the basis of the above rearings, together with numerous observations, the writers agree that *Aphidius testaceipes* does show a definite host preference and that many of the hosts accredited to *A. testaceipes* are undoubtedly factitious ones. Populations of Riverside hosts have been under surveillance for the past 3-years, and we conclude that the aphid hosts in this area seem to be preferred as follows:

Aphid species	Degree of control by parasite
1. *Aphis medicaginis* Koch	Excellent
2. *Aphis pseudohederae* Theob.	Excellent
3. *Aphis gossypii* Glover	Excellent
4. *Rhopalosiphum maidis* (Fitch)	Good
5. *Aphis rumicis* L.	Fair
6. *Aphis helianthi* Monell	Poor
7. *Myzus persicae* (Sulz.)	Poor

The last two species are not attacked often, and *Aphis helianthi* on *Pittosporum tobira* Ait. often produced nothing but dead larvae of *Aphidius testaceipes*. It is possible that both *A. helianthi* and *Myzus persicae* are attacked commonly by *A. testaceipes* only when they are in company with the more preferred host *Aphis gossypii*. This was frequently the case in our observations.

As mentioned above, in the section on *Aphidius chrysoaphidis*, *A. testaceipes* will not develop completely from the green citrus aphid, *Aphis spiraecola* Patch. Miller (1929) was the first to note that this parasite never developed from this aphid in Florida. Through the years many entomologists have contended that *Aphidius testaceipes* has not been an effective parasite on the several species of citrus aphids. In reality, effective control by this parasite is often present on citrus aphids such as *Aphis gossypii* Glover and *Toxoptera aurantii* (B. de Fonsc.), while *Aphis spiraecola* Patch is not parasitized. Thus *A. spiraecola* often builds up such high populations on citrus that the true parasitization picture is obscured, and no credit is given *Aphidius testaceipes* for keeping many of the other associated aphid species from becoming a problem.

Our observations show that this parasite never develops past the third instar in this aphid on citrus, *Spiraea* sp., *Viburnum suspensum* Lindl., *Pittosporum rhombifolia* Cunn., or *Pyracantha*

crento-serrata (Hance); yet this aphid is very attractive to the ovipositional instincts of *Aphidius testaceipes*. Hence *Aphis spiraecola* acts as a trap for *Aphidius testaceipes*, inasmuch as the numerous eggs deposited never developed into adult parasites. This parasite causes a certain amount of death to most *Aphis spiraeccla* populations each year, and several hundred dead aphids (with dead parasite larvae) have often been seen on one citrus terminal. It also seems well to note that *Charips* species readily oviposits in *Aphidius testaceipes* larvae in *Aphis spiraecola*, but these progeny are of course trapped and also die.

All recorded hosts of *Aphidius testaceipes* belong to the aphid tribe Aphidini, and most of the recorded host species belong to the genera *Aphis*, *Macrosiphum*, *Myzus*, and *Toxoptera*, in this order. This wide range of parasite specificity may occur, or it may be that *A. testaceipes* is a polytypic species each with several biological races. If the latter is true (and there is some indication of it, as noted above under *Aphidius pisivorus*), then it may be found that one strain attacks species of *Aphis*, another *Macrosiphum*, and so on.

A preliminary test was made by the authors with *Aphidius testaceipes* to see if F_1 progenies reared from an *Aphis* species would develop on other *Aphis* species. The results are summarized below. Several hundred male and female *A. testaceipes* were reared from field-collected individuals of *Aphis lutescens* Monell on *Nerium oleander* L. Of these, 20 mated females were placed with a population of *Aphis pseudohederae* Theob. on *Fatshedera* sp. The progenies of this rearing were placed similarly on *Aphis gossypii* Glover on *Hibiscus rosa-sinensis* L., and many male and female progenies were produced. Unfortunately, this experiment ended at this point, but at least good parasite production was effected in the laboratory by transferring the F_1 progeny from the original host to two different consecutive hosts.

Diaeretus rapae (M'Intosh)

Distribution.—Most of the United States (Muesebeck et al. 1951), New Brunswick (MacGillivray and Spicer 1953), and southern Canada (Krombein et al. 1958).

New Rearing Data.—About 100 individuals were reared from southern California aphid species from the following localities: Redlands, San Bernardino County, January 9, 1958, from *Myzus persicae* (Sulzer) on *Brassica oleracea* var. *capitata* L.; Riverside, March 31 and April 12, 1958, from *Myzus persicae* (Sulzer) on *Vinca minor* L.; Wheeler Ridge, Kern County, April 24, 1958, from *Brevicoryne brassicae* (L.) on *Brassica* sp.

Hyperparasites.—Four specimens of *Aphidencyrtus aphidivorus* (Mayr) were reared from the above sample taken on April 24. Several specimens of *Asaphes californicus* Girault also were reared from the Redlands and Riverside populations.

Diapause.—About 25% of the April 24th population were in diapause. Dissections made on June 20 indicated that these individuals were still in the last larval stage and quite active. The same was true of the April 12th population. Since none of the January or March populations contained any diapausing individuals, it appears as though *Diaeretus rapae* has a summer diapause in southern California.

Observations.—Many field observations showed that *Diaeretus rapae* was abundant in southern California during the winter and early spring on *Brevicoryne brassicae*, although in most cases individuals were not reared. Besides being an effective parasite of *B. brassicae*, *D. rapae* is one of the species most often seen attacking *Myzus persicae*. *D. rapae* frequently occurs in direct competition with *Ephedrus nitidus* Gahan, *Aphidius testaceipes* (Cresson), and *Aphelinus* sp. for the host *M. persicae*; yet this aphid is usually too abundant to be under satisfactory natural control. This would indicate that none of the parasites named above are well adapted to *M. persicae*, and that even all four species working together are unable to effect a great amount of natural control. Quite probably, then, *M. persicae* should be listed as a factitious host for these three parasite species.

Diaeretus salicaphis (Fitch)

Distribution.—California, Colorado, New York, Ohio, Utah (Muesebeck et al. 1951); New Brunswick ? (MacGillivray and Spicer 1953).

New Rearing Data.—About 80 specimens were reared from aphids collected at Riverside, California, on the following dates: September 17, 1957, from *Chaitophorus viminalis* Monell on *Salix* sp.; November 19, 1957, from *Chaitophorus* sp. on *Populus trichocarpa* T. and G. Two females were also reared from specimens collected at San Luis Rey Camp, San Diego County, June 12, 1958, from *Chaitophorus viminclis* Monell on *Salix* sp.

Hyperparasites.—We have one rather questionable record of rearing an encyrtid, *Psylledontus* species, from specimens collected at Riverside.

Diapause.—There was no indication of diapause in specimens of the above samples.

Observations.—*Diaeretus salicaphis* appears to be a common and rather effective parasite of *Chaitophorus viminalis* in southern California. There was no evidence of other Aphidiinae competing with *D. salicaphis* for this host; however, each sample gathered contained a number of predaceous dipterous larvae of the genus *Leucopis*.

Ephedrus californicus Baker

Distribution.—Arizona, California, Idaho, Oregon, Utah (Muesebeck et al. 1951); British Columbia (NEW RECORD).

New Rearing Data.—Ten specimens were reared from aphids collected in southern California and British Columbia as follows: Five males and females, Glendale, Los Angeles County, California, April 15, 1957, from *Macrosiphum rosae* (L.) on *Rosa* sp.; and five males and females from Skihist Camp, nr. Lytton, British Columbia, June 2, 1957, from *Macrosiphum ambrosiae* (Thomas) on *Baccharis* sp.

Hyperparasites.—None were reared from the above samples.

Diapause.—Not apparent in the above samples.

Observations.—*Ephedrus californicus* appears to be an important parasite of *Macrosiphum rosae* in coastal California; however, it has not been reared from this aphid in the drier, warmer Riverside area. The British Columbia *Ephedrus* sample was collected, together with *Aphidius ohioensis* and *Trioxys schlingeri*, and of the total of over 150 specimens of parasites reared, only 5 were *E. californicus*. Although this species has never been reared in abundance, we have collected large series of emerged cocoons of what was believed to be this species from Glendale, Altadena, and Pasadena, all in coastal Los Angeles County, on *M. rosae*. This species appears to be somewhat specific to species of *Macrosiphum*, but there is one record on a species of *Rhopalosiphum*.

Ephedrus nitidus Gahan

Distribution.—Ontario, Canada, to Virginia; Ohio, California (Muesebeck et al. 1951), and British Columbia (Krombein et al. 1958).

New Rearing Data.—Twenty-five specimens of *Ephedrus nitidus* were reared from aphids collected at Riverside, California, on the following dates: April 8, 1957, from *Aphis gossypii* Glover on *Citrus sinensis* (L.) Osbeck; January 6 and March 31, 1958, from *Myzus persicae* (Sulzer) on *Vinca minor* L.; January 21, 1958, from *M. persicae* on *Malva parviflora* L.; February 27, 1958, from *M. persicae* on *Viburnum suspensum* Lindl., and April 26, 1958, from *Aphis* sp. on *Foeniculum vulgare* (L.).

Hyperparasites.—*Aphidencyrtus aphidivorus* (Mayr) was reared from *Ephedrus nitidus* on March 31.

Diapause.—The only evidence of diapause appeared in the March 31 sample. When dissections were made on June 26, 1958, about 25% of the cocoons were found to contain living diapause larvae. It is possible, therefore, that *Ephedrus nitidus* has a summer diapause in Riverside.

Observations.—Our records indicate that *Ephedrus nitidus*, along with *Diaeretus rapae*, appear to prefer *M. persicae* as a host. Besides species of *Myzus* and *Aphis* this parasite also attacks a *Macrosiphum* species.

Praon occidentalis Baker

Distribution.—California, Idaho, Nevada, Oregon, and Ontario, Canada (Muesebeck et al., 1951), New Brunswick (MacGillivray and Spicer 1953), and Wisconsin (Krombein et al. 1958).

New Rearing Data.—Although more than 100 cocoons of this species have been collected from *Macrosiphum rosae* (L.) at Riverside, California, only 2 yielded adult parasites; another 35 gave only hyperparasites, and the remaining ones were found to be in diapause. The two individuals of *P. occidentalis* reared from *M. rosae* emerged on March 21 and March 31, 1958. Two individuals were reared from *Macrosiphum pisi* (Harris) on *Medicago sativa* L. at Colton, San Bernardino County, April 12, 1957, and three others were reared from the same host at Riverside on May 22, 1958. Several hundred specimens were reared from *M. pisi* in our insectaries when field-parasitized aphids were brought into the laboratory to be used for stock cultures.

Hyperparasites.—About 30% of all cocoons collected from *Rosa* sp. produced *Asaphes californicus* Girault, *Pachyneuron siphonophorae* (Ashmead), or one of several *Charips* species.

Diapause.—The diapause situation for *Praon occidentalis* at Riverside has been discussed by Schlinger (1960). Suffice it to say that this species when parasitizing *Macrosiphum rosae*, begins diapause in the F_1 generation in March, and each generation thereafter shows an increasing amount of diapause and hyperparasitism (see discussion also under *Praon unicus*).

Observations.—*Praon occidentalis* is apparently not common in southern California. This may be due to the high degree of diapause during the early generations. It has, however, at two different times become a pest on laboratory cultures of *Macrosiphum pisi* that were being reared for other species of parasites. Although *P. occidentalis* apparently has the ability to parasitize *M. pisi* heavily in the laboratory, in the field it has been only rarely encountered during the years 1956 to 1958.

Praon palitans Muesebeck

Praon palitans Muesebeck 1956, Bull. Brooklyn Ent. Soc. 51: 27, fig. 2.

Distribution.—Italy, France, Israel, Yugoslavia, and Kentucky (Muesebeck 1956); Turkey, Lebanon, and Iran (van den Bosch 1957); California (van den Bosch et al. 1957); Arizona, Nevada, New Mexico (Schlinger and Hall 1959); Utah (Benjamin Puttler, USDA, in conversation).

Hyperparasites.—*Asaphes californicus* Girault, *Pachyneuron siphonophorae* (Ashmead), *Aphidencyrtus aphidivorus* (Mayr), and several species of *Charips* have been reared from *Praon palitans*.

Diapause.—A distinct facultative diapause usually occurs in *Praon palitans* from October to

March. This condition has been discussed recently in some detail by Schlinger and Hall (1959, 1960).

Observations.—This species was imported, colonized, and established in California during the period from 1956 to 1957 from material collected in the European and Middle Eastern countries named above (see van den Bosch et al. 1959a) in an effort to bring the new pest aphid, *Therioaphis maculata* (Buckton), under biological control. A synopsis of the biology of *Praon palitans* was given by Schlinger and Hall (1959). This was followed by a more thorough biological treatment by these authors (1960). The role of this parasite in the biological control of *T. maculata* was reported by van den Bosch et al. (1959b). Suffice it to say that in most areas under study this parasite has been very effective against *T. maculata*.

Praon simulans (Provancher)

Distribution.—Southern Canada and northern United States (Muesebeck et al. 1951).

New Rearing Data.—About 25 specimens have been reared from *Macrosiphum pisi* (Harris) on *Medicago sativa* L. in several localities in Kern and Inyo counties, California, collected mostly in March, April, or September, 1957 and 1958.

Hyperparasites.—Several individuals of *Pachyneuron siphonophorae* (Ashmead) were reared from the Kern County specimens.

Diapause.—A definite diapause was observed in *Praon simulans*, from November through March, in the field. Several diapause specimens that were collected in March and April have also been examined. These diapause larvae were still alive when dissections were made in the laboratory in March 1958. Apparently *P. simulans* exhibits a spring and/or winter diapause, at least in Kern County, California, and these factors alone may explain why *P. simulans* is a sporadically effective parasite on *Macrosiphum pisi* in this area.

Observations.—*Praon simulans* has been encountered only as a parasite of *Macrosiphum pisi*, and only twice (in March and October, 1957) has it been present in numbers. In Kern County, California, it does not appear to be a continuously effective parasite. This species probably does not occur in California south of the Tehachapi Mountains, and references to it from this southern area pertain either to *Praon unicus* or to *Praon occidentalis*.

Praon unicus Smith

Distribution.—Colorado (Smith 1944); Washington (Krombein et al. 1958), and California (NEW RECORD).

New Rearing Data.—*Praon unicus* is the *Praon* species most common in Riverside, and nearly 100 individuals have been reared from the following aphids: March 12, 1957, from *Aphis rumicis* L. on *Rumex crispus* L.; March 3, 1958, from *Phorodon menthae* (Buckton) on *Mentha arvensis* L.; March 25 and April 14, 1957, April 4 and 17, 1958, from *Macrosiphum ambrosiae* (Thomas) on *Abelia* sp. (a hybrid called *Gaucheri*); January 21, 1958, from *Myzus persicae* (Sulzer) on *Mirabilis laevis* (Benth.), and January 22, 1958, from *M. persicae* on *Spinacia oleracea* L.; February 27, 1958, from *Aphis* sp. on *Pyracantha crenatoserrata* (Hance); March 24, April 10, 17, and 25, 1958, from *Macrosiphum rosae* (L.) on *Rosa* sp.

Hyperparasites.—*Asaphes californicus* Girault, *Pachyneuron siphonophorae* (Ashmead), and several *Charips* species were reared from the above samples.

Diapause.—A definite facultative summer diapause is associated with *Praon unicus* in Riverside, California. Rearings supplemented by field observations revealed that on both *Macrosiphum rosae* and *M. ambrosiae* this parasite begins diapause with the first generation of these hosts (Schlinger 1960) and continues producing more and more diapause individuals until some time in June, when all individuals appear to be in diapause. The hyperparasitic *Charips* species also go into diapause, but often emerge in the laboratory in about 6 months, whereas dissections of *P. unicus* show them to remain as living, fully developed larvae for a year or more or to die before emerging.

Observations.—This is undoubtedly a very important aphid parasite in southern California, due primarily to the fact that it possesses a summer diapause which tides the parasite over the long hot summer period when aphids are not present in any number.

Trioxys (Acanthocaudus) schlingeri Muesebeck

Trioxys (Acanthocaudus) schlingeri Muesebeck 1958, Ent. News, 69: 144, fig. 3.

Distribution.—Known only from the type locality in British Columbia.

Observations.—The type series contained about 80 specimens, all reared from *Macrosiphum ambrosiae* (Thomas) on *Baccharis* sp. No diapause was evident with this population, nor were any hyperparasites reared. This is the third known species of the subgenus, all of which are known to attack only species of *Macrosiphum*.

Trioxys (Trioxys) utilis Muesebeck

Trioxys utilis Muesebeck 1956, Bull. Brooklyn Ent. Soc., 51: 26, fig. 1.

Distribution.—Italy, France, Kentucky, and Nebraska (Muesebeck 1956); Iraq, Iran, Israel, and Turkey (van den Bosch 1957); California (van den Bosch et al. 1957); Arizona, Nevada (Schlinger and Hall 1959); Mexicali Valley Mexico (Benjamin Puttler, USDA, in conversation).

Hyperparasites.—*Asaphes californicus* Girault, *Pachyneuron siphonophorae* (Ashmead), *Aphiden-*

cyrtus aphidivorus (Mayr), and several *Charips* species have been reared from individuals collected in California.

Diapause.—Up until 1958 (Schlinger and Hall 1959) it was thought that *Trioxys utilis* did not have a diapause. Detailed winter studies in southern California indicated that *Trioxys* adults were active throughout this period. Although this species was noticeably absent in Imperial Valley, California, during the summer months, it was judged to be simply reflecting the low host density of that period. However, in the spring of 1959 there was an almost "spontaneous" occurrence of adult *Trioxys* in Imperial Valley. These adults were known not to have been building up in the fields that were being studied, and it was concluded that they must have emerged from diapause. There is growing evidence that diapause is induced in that area in late spring and early summer and that these individuals emerge the following fall, winter, or spring, emergence depending on weather conditions. Further investigations concerning diapause in in *T. utilis* are under way.

Observations.—*Trioxys utilis*, like *Praon palitans*, was imported into California to aid in the biological control of *Therioaphis maculata* (Buckton). A synopsis of the biology of this parasite has been given by Schlinger and Hall (1959), and the colonization and evaluation have been reported by van den Bosch et al. (1959a, 1959b). This is an extremely important parasite of *Therioaphis maculata*, particularly in the hot Imperial Valley of California.

Trioxys (**Trioxys**) sp.

On August 11, 1958, the authors found a light population of *Trioxys* cocoons on *Salix* sp. at Lake Hughes, Los Angeles County, California. Neither the aphid host (*Cavariella* sp.) nor the parasite cocoons was abundant at this time. Altogether, about 50 cocoons were gathered and brought to the laboratory. Within a week four males and females had emerged, but with them emergence ceased. Dissections 2 months later revealed many dead larvae and pupae, but also a few live larvae. This would indicate that part of the *Trioxys* population was in a state of summer diapause at that time.

This species was identified by the authors as a new species, and this finding was later verified as such by C. F. W. Muesebeck.

CALIFORNIA PARASITES (APHIDIINAE) AND THEIR APHID HOSTS

Previously recorded hosts from which parasites were reared and reported by the authors in this text are preceded by an asterisk (*). Hosts include some which have been reported only outside of California.

1. **Aphidius (Aphidius) alius** Muesebeck
   **Macrosiphum rosae* (Linnaeus) [Muesebeck 1958]
2. **Aphidius (Aphidius) avenaphis** (Fitch)
   Macrosiphum cerealis Kaltenbach (?) [Gahan 1911]
   Macrosiphum granarium (Kirby) [Smith 1944]
   Myzus persicae (Sulzer) [Smith 1944]
   Rhopalosiphum fitchii (Sanderson) [Gahan 1911]
   Rhopalosiphum prunifoliae (Fitch) [Muesebeck et al. 1951]
3. **Aphidius (Aphidius) confusus** Ashmead
   Macrosiphum sp. [Muesebeck et al. 1951]

   NEW HOSTS:
   Macrosiphum sp.
   Macrosiphum rosae (Linnaeus)
   Macrosiphum rudbeckiae (Fitch)
4. **Aphidius (Aphidius) nigripes** Ashmead [NEW CALIFORNIA RECORD]
   Aphis abbreviata Patch [MacGillivray and Spicer 1953]
   Capitophorus sp. [Shands et al. 1955]
   Macrosiphum dirhodum (Walker) [Smith 1944]
   Macrosiphum granarium (Kirby) [Gahan 1911]
   Macrosiphum liriodendri (Monell) [Smith 1944]
   Macrosiphum solanifolii (Ashmead) [Smith 1944]
   Myzus persicae (Sulzer) [MacGillivray and Spicer 1953]

   NEW HOST:
   Macrosiphum rosae (Linnaeus) [questioned by Smith 1944]
5. **Aphidius (Aphidius) nigriteleus** Smith
   Aphis abbreviata Patch [Shands et al. 1955]
   Capitophorus sp. [Shands et al. 1955]
   Macrosiphoniella sanborni (Gillette) [Smith 1944]
   Macrosiphum fridicola (Gillette and Palmer) [MacGillivray and Spicer 1953]
   Macrosiphum rosae (Linnaeus) [MacGillivray and Spicer 1953]
   Macrosiphum solanifolii (Ashmead) [Shands et al. 1955]
   **Myzus persicae* (Sulzer) [Smith 1944]
   Myzus solani (Kaltenbach) [Shands et al. 1955]
   Rhopalosiphum rufomaculatum (Wilson) [Smith 1944]

   NEW HOSTS:
   Aphis helianthi Monell
   Aphis rumicis Linnaeus
   Macrosiphum rudbeckiae (Fitch)
   Phorodon menthae (Buckton)
6. **Aphidius (Aphidius) pisivorus** Smith [NEW CALIFORNIA RECORD]
   Aphis abbreviata Patch [MacGillivray and Spicer 1953]
   Macrosiphum erigeronensis (Thomas) [Krombein et al. 1958]
   Macrosiphum pisi (Harris) [Smith 1944]
   Macrosiphum solanifolii (Ashmead) [MacGillivray and Spicer 1953]
   Myzus persicae (Sulzer) [MacGillivray and Spicer 1953]

   NEW HOST:
   Macrosiphum albifrons Essig
7. **Aphidius (Aphidius) pterocommae** Ashmead
   Clavigerus populifoliae (Fitch) [MacGillivray and Spicer 1953]
   Clavigerus smithae (Monell) [Smith 1944]
   Clavigerus sp. [Smith 1944]
   Lachnus saliciola (Uhler) [Gahan 1911]
   **Pterocomma bicolor* (Oestlund) [Smith 1944]
8. **Aphidius (Lysiphlebus) chrysoaphidis** Smith [NEW CALIFORNIA RECORD]
   Aphis chrysothamni Wilson [Smith 1944]
   Aphis gregalis Knowlton [Smith 1944]

   NEW HOSTS:
   Aphis gossypii Glover
   Aphis helianthi Monell
   Aphis heraclella Davis
   Aphis lutescens Monell

Aphis pseudohederae Theobald
Aphis sp.

9. **Aphidius (Lysiphlebus) testaceipes** (Cresson)
(Recorded hosts from Muesebeck et al. 1951, unless otherwise stated.)
Aphis abbreviata Patch [MacGillivray and Spicer 1953]
Aphis cerasifoliae Fitch
**Aphis gossypii* Glover
**Aphis helianthi* Monell
Aphis heraclella Davis
Aphis laburni Kaltenbach
**Aphis medicaginis* Koch
Aphis neogillettei Palmer
Aphis nerii Boyer de Fonscolombe
Aphis oenotherae Oestlund
Aphis oestlundi Gillette
Aphis phaceliae Gillette and Palmer
**Aphis rumicis* Linnaeus
Aphis saliceti Kaltenbach
Aphis sp. (?) *neomexicana* (Cockerell) [MacGillivray and Spicer 1953]
Brevicoryne brassicae (Linnaeus)
Capitophorus ribis (Linnaeus)
Hysteroneura setariae (Thomas)
Macrosiphum citrifolii (Ashmead)
Macrosiphum cucurbitae (Thomas)
Macrosiphum granarium (Kirby)
Macrosiphum rosae (Linnaeus)
Myzus cerasi (Fabricius)
**Myzus persicae* (Sulzer)
Myzus rhamni Boyer de Fonscolombe
**Rhopalosiphum maidis* (Fitch)
Rhopalosiphum prunifoliae (Fitch)
Toxoptera aurantii (Boyer de Fonscolombe)
Toxoptera graminum (Rondani)
NEW HOSTS:
Aphis lutescens Monell
Aphis pseudohederae Theobald
Macrosiphum ambrosiae (Thomas)

10. **Aphidius (Protaphidius) californicus** Ashmead
Cinara occidentalis (Davidson) [Smith 1944]
Eulachnus agilis (Kaltenbach) [?MacGillivray and Spicer 1953]
Schizolachnus pini-radiatae (Davidson) [Smith 1944]

11. **Aphidius (Protaphidius) nigrovarius** Provancher
Lachnus sp. [Gahan 1911]

12. **Diaeretus chenopodiaphidis** (Ashmead)
Aphis rumicis Linnaeus [MacGillivray and Spicer 1953]
Hyalopterus atriplicis (Linnaeus) [Smith 1944]

13. **Diaeretus fuscicornis** (Ashmead)
Aphis forbesi Weed [Smith 1944]

14. **Diaeretus rapae** (M'Intosh)
Aphis abbreviata Patch [MacGillivray and Spicer 1953]
**Brevicoryne brassicae* (Linnaeus) [Gahan 1911]
Calaphis betulacecolens (Fitch) [MacGillivray and Spicer 1953]
Capitophorus sp. [Shands et al. 1955]
Euceraphis betulae (Koch) [MacGillivray and Spicer 1953]
Macrosiphum solanifolii (Ashmead) [Shands et al. 1955]
**Myzus persicae* (Sulzer) [Smith 1944]
Rhopalosiphum pseudobrassicae (Davis) [Smith 1944]

15. **Diaeretus salicaphis** (Fitch)
Aphis helianthi Monell [?MacGillivray and Spicer 1953]
**Chaitophorus viminalis* Monell [Smith 1944]
Clavigerus populifoliae (Fitch) [?MacGillivray and Spicer 1953]
Periphyllus populicola (Thomas) [Gahan 1911]

16. **Ephedrus aestivalis** Viereck
Recorded host: none.

17. **Ephedrus californicus** Baker
**Macrosiphum ambrosiae* (Thomas) [Smith 1944]
Macrosiphum pisi (Harris) [Smith 1944]
**Macrosiphum rosae* (Linnaeus) [Smith 1944]
Macrosiphum sp. [Smith 1944]
Rhopalosiphum grabhami Cockerell [Smith 1944]

18. **Ephedrus nitidus** Gahan
Macrosiphum solanifolii (Ashmead) [Smith 1944]
**Myzus persicae* (Sulzer) [Smith 1944]
Myzus cerasi (Fabricius) [Krombein et al. 1958]
NEW HOSTS:
Aphis gossypii Glover
Aphis sp.

19. **Monoctonus paulensis** (Ashmead)
Macrosiphum pisi (Harris) [Smith 1944]

20. **Monoctonus secundus** Viereck
Recorded host: none.

21. **Praon occidentalis** Baker
**Macrosiphum pisi* (Harris) [Smith 1944]
Macrosiphum solanifolii (Ashmead) [MacGillivray and Spicer 1953]
Macrosiphum sp. [Smith 1944]
Myzus persicae (Sulzer) [MacGillivray and Spicer 1953]
NEW HOSTS:
Macrosiphum rosae (Linnaeus)

22. **Praon palitans** Muesebeck
**Therioaphis maculata* Buckton [van den Bosch 1957]
**Therioaphis riehmi* (Börner) [Schlinger and Hall 1959]
Therioaphis trifolii (Monell) [Muesebeck 1956]

23. **Praon simulans** (Provancher)
Macrosiphum albifrons Essig [MacGillivray and Spicer 1953]
**Macrosiphum pisi* (Harris) [Smith 1944]
Macrosiphum solanifolii (Ashmead) [MacGillivray and Spicer 1953]
Myzus persicae (Sulzer) [Shands et al. 1955]

24. **Praon unicus** Smith [NEW CALIFORNIA RECORD]
Recorded hosts: none.
NEW HOSTS:
Aphis rumicis Linnaeus
Macrosiphum ambrosiae (Thomas)
Macrosiphum rosae (Linnaeus)
Macrosiphum sp.
Myzus persicae (Sulzer)
Phorodon menthae (Buckton)

25. **Trioxys (Trioxys) cupressicola** Gahan
Cerosipha sp. [Gahan 1919]

26. **Trioxys (Trioxys) utilis** Muesebeck
**Therioaphis maculata* (Buckton) [van den Bosch 1957]
**Therioaphis riehmi* (Börner) [Schlinger and Hall 1959]
Therioaphis trifolii (Monell) [Muesebeck 1956]

APHID SPECIES AND THE PARASITES (APHIDIINAE) IN CALIFORNIA

Although some of the aphid species listed here do not occur in California, it seemed advisable to list all species that are attacked by the California Aphidiinae.

1. **Aphis abbreviata** Patch
Aphidius (*Aphidius*) *nigripes* Ashmead
Aphidius (*Aphidius*) *nigriteleus* Smith
Aphidius (*Aphidius*) *pisivorus* Smith
Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
Diaeretus rapae (M'Intosh)

2. **Aphis cerasifoliae** Fitch
Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)

3. **Aphis chrysothamni** Wilson
Aphidius (*Lysiphlebus*) *chrysoaphidis* Smith

4. **Aphis forbesi** Weed
Diaeretus fuscicornis (Ashmead)

5. **Aphis gossypii** Glover
   Aphidius (*Lysiphlebus*) *chrysoaphidis* Smith
   Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
   Ephedrus nitidus Gahan
6. **Aphis gregalis** Knowlton
   Aphidius (*Lysiphlebus*) *chrysoaphidis* Smith
7. **Aphis helianthi** Monell
   Aphidius (*Aphidius*) *nigriteleus* Smith
   Aphidius (*Lysiphlebus*) *chrysoaphidis* Smith
   Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
   Diaeretus salicaphis (Fitch) (?)
8. **Aphis heraclella** Davis
   Aphidius (*Lysiphlebus*) *chrysoaphidis* Smith
   Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
9. **Aphis laburni** Kaltenbach
   Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
10. **Aphis lutescens** Monell
    Aphidius (*Lysiphlebus*) *chrysoaphidis* Smith
    Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
11. **Aphis medicaginis** Koch
    Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
12. **Aphis neogillettei** Palmer
    Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
13. **Aphis neomexicana** (Cockrell) (?)
    Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
14. **Aphis nerii** Boyer de Fonscolombe
    Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
15. **Aphis oenotherae** Oestlund
    Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
16. **Aphis oestlundi** Gillette
    Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
17. **Aphis phaceliae** Gillette and Palmer
    Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
18. **Aphis pseudohederae** Theobald
    Aphidius (*Lysiphlebus*) *chrysoaphidis* Smith
    Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
19. **Aphis rumicis** Linnaeus
    Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
    Diaeretus chenopodiaphidis (Ashmead)
    Praon unicus Smith
20. **Aphis saliceti** Kaltenbach
    Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
21. **Aphis** species
    Aphidius (*Lysiphlebus*) *chrysoaphidis* Smith
    Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
    Ephedrus nitidus Gahan
22. **Brevicoryne brassicae** (Linnaeus)
    Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
    Diaeretus rapae (M'Intosh)
23. **Calaphis betulaecolens** (Fitch)
    Diaeretus rapae (M'Intosh)
24. **Capitophorus ribis** (Linnaeus)
    Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
25. **Capitophorus** species
    Aphidius (*Aphidius*) *nigripes* Ashmead
    Aphidius (*Aphidius*) *nigriteleus* Smith
    Diaeretus rapae (M'Intosh)
26. **Cavariella** species
    Trioxys (*Trioxys*) sp.
27. **Cerosipha** species
    Trioxys cupressicola Gahan
28. **Chaitophorus viminalis** Monell
    Diaeretus salicaphis (Fitch)
29. **Cinara occidentalis** (Davidson)
    Aphidius (*Protaphidius*) *californicus* Ashmead
30. **Cinara** species
    Aphidius (*Protaphidius*) *ponderosae* Muesebeck
31. **Clavigerus populifoliae** (Fitch)
    Aphidius (*Aphidius*) *pterocommae* Ashmead
    Diaeretus salicaphis (Fitch)
32. **Clavigerus smithae** (Monell)
    Aphidius (*Aphidius*) *pterocommae* Ashmead
33. **Clavigerus** species
    Aphidius (*Aphidius*) *pterocommae* Ashmead
34. **Euceraphis betulae** (Koch)
    Diaeretus rapae (M'Intosh)
35. **Eulachnus agilis** (Kaltenbach) (?)
    Aphidius (*Protaphidius*) *californicus* Ashmead
36. **Hyalopterus atriplicis** (Linnaeus)
    Diaeretus chenopodiaphidis (Ashmead)
37. **Hysteroneura setariae** (Thomas)
    Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
38. **Lachnus saliciola** (Uhler)
    Aphidius (*Protaphidius*) *pterocommae* Ashmead
39. **Lachnus** species
    Aphidius (*Protaphidius*) *nigrovarius* Provancher
40. **Macrosiphoniella sanborni** (Gillette)
    Aphidius (*Aphidius*) *nigriteleus* Smith
41. **Macrosiphum albifrons** Essig
    Aphidius (*Aphidius*) *pisivorus* Smith
    Praon simulans (Provancher)
42. **Macrosiphum ambrosiae** (Thomas)
    Aphidius (*Lysiphlebus*) *testaceipes* (Cresson) (?)
    Ephedrus californicus Baker
    Praon unicus Smith
43. **Macrosiphum cerealis** Kaltenbach (?)
    Aphidius (*Aphidius*) *avenaphis* (Fitch)
44. **Macrosiphum citrifolii** (Ashmead)
    Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
45. **Macrosiphum cucurbitae** (Thomas)
    Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
46. **Macrosiphum dirhodum** (Walker)
    Aphidius (*Aphidius*) *nigripes* Ashmead
47. **Macrosiphum erigeronensis** (Thomas)
    Aphidius (*Aphidius*) *pisivorus* Smith
48. **Macrosiphum fridicola** (Gillette and Palmer)
    Aphidius (*Aphidius*) *nigriteleus* Smith
49. **Macrosiphum granarium** (Kirby)
    Aphidius (*Aphidius*) *avenaphis* (Fitch)
    Aphidius (*Aphidius*) *nigripes* Ashmead
50. **Macrosiphum illini** Hottes and Frison
    Aphidius (*Aphidius*) *ohioensis* Smith
51. **Macrosiphum liriodendri** (Monell)
    Aphidius (*Aphidius*) *nigripes* Ashmead
52. **Macrosiphum pisi** (Harris)
    Aphidius (*Aphidius*) *pisivorus* Smith
    Ephedrus californicus Baker
    Monoctonus paulensis (Ashmead)
    Praon occidentalis Baker
    Praon simulans (Provancher)
53. **Macrosiphum rosae** (Linnaeus)
    Aphidius (*Aphidius*) *alius* Muesebeck
    Aphidius (*Aphidius*) *confusus* Ashmead
    Aphidius (*Aphidius*) *nigripes* Ashmead
    Aphidius (*Aphidius*) *nigriteleus* Smith
    Ephedrus californicus Baker
    Praon occidentalis Baker
    Praon unicus Smith
54. **Macrosiphum rudbeckiae** (Fitch)
    Aphidius (*Aphidius*) *confusus* Ashmead
    Aphidius (*Aphidius*) *nigriteleus* Smith
55. **Macrosiphum** species
    Aphidius (*Aphidius*) *confusus* Ashmead
    Ephedrus californicus Baker
    Praon occidentalis Baker
    Praon unicus Smith
56. **Myzus cerasi** (Fabricius)
    Aphidius (*Aphidius*) *testaceipes* (Cresson)
    Ephedrus nitidus Gahan
57. **Myzus persicae** (Sulzer)
    Aphidius (*Aphidius*) *avenaphis* (Fitch)
    Aphidius (*Aphidius*) *nigripes* Ashmead
    Aphidius (*Aphidius*) *nigriteleus* Smith
    Aphidius (*Aphidius*) *pisivorus* Smith
    Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
    Diaeretus rapae (M'Intosh)
    Ephedrus nitidus Gahan
    Praon occidentalis Baker
    Praon simulans (Provancher)
    Praon unicus Smith
58. **Myzus rhamni** Boyer de Fonscolombe
    Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
59. **Myzus solani** (Kaltenbach)
    Aphidius (*Aphidius*) *nigriteleus* Smith
60. **Periphyllus populicolus** (Thomas)
    Diaeretus salicaphis (Fitch)

61. **Phorodon menthae** (Buckton)
Aphidius (*Aphidius*) *nigriteleus* Smith
Praon unicus Smith
62. **Pterocomma bicolor** (Oestlund)
Aphidius (*Aphidius*) *pterocommae* Ashmead
63. **Rhopalosiphum fitchii** (Sanderson)
Aphidius (*Aphidius*) *avenaphis* (Fitch)
64. **Rhopalosiphum grabhami** Cockerell
Ephedrus californicus Baker
65. **Rhopalosiphum maidis** (Fitch)
Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
66. **Rhopalosiphum prunifoliae** (Fitch)
Aphidius (*Aphidius*) *avenaphis* (Fitch)
Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)
67. **Rhopalosiphum pseudobrassicae** (Davis)
Diaeretus rapae (M'Intosh)
68. **Rhopalosiphum rufomaculatum** (Wilson)
Aphidius (*Aphidius*) *nigriteleus* Smith
69. **Schizolachnus pini-radiatae** (Davidson)
Aphidius (*Protaphidius*) *californicus* Ashmead
70. **Therioaphis maculata** (Buckton)
Praon palitans Muesebeck
Trioxys (*Trioxys*) *utilis* Muesebeck
71. **Therioaphis riehmi** (Börner)
Praon palitans Muesebeck
Trioxys (*Trioxys*) *utilis* Muesebeck
72. **Therioaphis trifolii** (Monell)
Praon palitans Muesebeck
Trioxys (*Trioxys*) *utilis* Muesebeck
73. **Toxoptera aurantii** (Boyer de Fonscolombe)
Aphidius (*Lysiphelbus*) *testaceipes* (Cresson)
74. **Toxoptera graminum** (Rondani)
Aphidius (*Lysiphlebus*) *testaceipes* (Cresson)

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A REVIEW OF THE GENUS EULONCHUS GERSTAECKER. PART I. THE SPECIES OF THE SMARAGDINUS GROUP (DIPTERA: ACROCERIDAE)[1]

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ABSTRACT

This species group includes only *Eulonchus smaragdinus* Gerstaecker (the generic type) and *E.* **halli.** The latter occurs in southern California, the former ranges from Lake County southward through California into northern Baja California; though sympatric, the two species do not appear synchronously. A subspecies, *E. smaragdinus* **pilosus,** also occurs in southern California but has not been found together with the nominate form *E. s. smaragdinus*. The egg and first-instar larva of *E. halli* are the first to be described for any *Eulonchus*, and are similar to these stages in species of *Ogcodes* Latr. that are parasites of spiders. An apparent case of mutualism is noted between *E. halli* and its nectar source, the plant *Cryptantha intermedia* Greene (Boraginaceae).

A study of the genus *Eulonchus* Gerstaecker was undertaken in 1950 as part of a project on the revision of the family Acroceridae (=Cyrtidae).[2] Due to the scope of this revision it seemed advisable first to publish the descriptions of the several new genera and new species encountered during the study. This is the eighth in a series of articles concerning this revision. Others which have been published or are in press include those for 1953, 1956, 1959, 1960a, b, c, d. Biological data have been excluded from most of these articles (except *Ogcodes*, 1960a), since a separate paper is planned for the biology of the Acroceridae.

The present article concerns the diagnosis of the genus *Eulonchus* Gerstaecker, the definition of the *smaragdinus* group, and the description of the new subspecies *E. smaragdinus pilosus* and the new species *E. halli*. The figures were prepared by the author with the aid of a camera lucida.

Eulonchus Gerstaecker

Eulonchus Gerstaecker 1856, Stettin. Ent. Zeit. 17: 360; Cole 1919, Trans. Amer. Ent. Soc. 45: 31; Sabrosky 1948, Amer. Midland Nat. 39: 388.

Type species.—*Eulonchus smaragdinus* Gerstaecker, by monotypy.

Diagnosis.—Large flies (8–14 mm.) usually unicolorous metallic green or blue with tinges of purple or brown and with yellow or brown legs. Antennae long; segments I and II short, III at least twice as long as I and II combined; antennae inserted about in middle of head, antennal triangle minute; ocellar tubercle nearly flat to well raised with median or lateral projections, usually with three distinct ocelli; eyes pilose and contiguous or nearly so below and usually above antennae; proboscis well developed reaching to end of thorax to well beyond tip of abdomen; maxillary palpus present; wing venation strong, veins prominent and all cells complete; male genitalia terminal, consisting of well-developed claspers and a large aedeagus which usually has a distinct, subapical, gonoporal notch.

Species and subspecies now included in *Eulonchus* are *E. halli* Schlinger n. sp., *E. marialiciae* Brimley, *E. marginatus* Osten Sacken, *E. sapphirinus* Osten Sacken, *E. smaragdinus smaragdinus* Gerstaecker, *E. smaragdinus pilosus* Schlinger n. subsp., and *E. tristis* Loew. As now understood, most of these species represent species groups.

SPECIES OF THE *smaragdinus* GROUP

This species group contains two species, *halli* Schlinger n. sp. and *smaragdinus* Gerstaecker, which are characterized by having a curved proboscis, a sharply acuminate terminal antennal segment (female only), eyes contiguous above and below antennae, a frontal triangle which is glabrous and polished, and whose basal margins are lined with short, indistinct hairs, a short and broad abdomen, a long and narrow aedeagus, and a cup-shaped basistylus with a long, narrow, double-pronged, acuminate dististylus.

Nothing is known about the hosts of these species, but the author presumes that certain avicularoid spiders will be found to be their hosts.

The two species of this group can be separated as follows:

A. Ocellar tubercle well developed and bifurcated; proboscis shorter than wing length; labellum about one-half as long as anteclypeus; legs dark brown and black . . . . . **halli** Schlinger, n. sp.

B. Ocellar tubercle nearly flat and weakly bifurcated; proboscis as long as or longer than wing length; labellum about as long as anteclypeus; legs mostly bright yellow . . . . . **smaragdinus** Gerstaecker

Eulonchus smaragdinus Gerstaecker

Eulonchus smaragdinus Gerstaecker 1856, Stettin. Ent. Zeit. 17: 360.

Male.—Lengths of entire specimens range from 8 to 14 mm.; wing lengths 6 to 12 mm. Color of

[1]Accepted for publication November 9, 1959.

[2]A thesis entitled "A generic revision and catalogue of the Acroceridae (Diptera)" was submitted to the University of California at Davis in 1957 in partial fulfillment of the requirements for the degree Doctor of Philosophy.

body varying from metallic green to blue, occasional specimens with purple reflections or all-purple abdomens; legs bright yellow with only the coxae metallic green or blue, tarsi light brown. Pile golden yellow or yellowish-white, rarely with light brown inflections. Proboscis longer than wing length, usually surpassing apex of abdomen. Labellum as long as anteclypeus; ocellar tubercle triangular and flattened; terminal antennal segment usually bearing one to five (commonly two to three) minute setae along the truncate, apical margin, and with four small sensorial pits along the inner margin. Aedeagus (fig. 1) with a large, C-shaped gonoporal notch.

Female.—Lengths of entire specimens range from 8 to 12 mm., wing lengths 8 to 12 mm. About as in the male described above except that the antennae are sharply acuminate and contain one to three (usually two) apical setae.

Distribution.—This species is apparently restricted from about the 39th parallel in northern California to the 31st parallel in northern Baja California, Mexico. It is commonly found along coastal California, but is rarely encountered in the central Sierra Nevada Mountains.

In regard to the distribution of this species, it seems important to note that Brunetti (1926) recorded a specimen from Cerro Colorado, Dept. de Florida, URUGUAY, as this species. Since no other record of the genus is known from outside the Nearctic region, and since many South American species of the genus *Lasia* Wiedemann are superficially like *Eulonchus* species, I believe Brunetti actually saw a species of *Lasia*. According to authorities in the Paris Museum, Brunetti's specimen of *E. smaragdinus* is presumably lost.

Sabrosky (1948) noted that Dr. Aldrich had recorded this species from Utah in his card file. I have not seen any specimens from Utah, and it seems probable that Aldrich actually saw a specimen of *E. sapphirinus* Osten Sacken (with an extended proboscis), which is not an uncommon species in northern Utah.

Discussion.—An examination of 349 specimens of this species has revealed considerable variation in the coloration of the various populations, but there are some indications that specimens in northern California represent, or are evolving a form distinct from that throughout most of southern California and Baja California. However, the only discrete subspecies appears to be the new one described below from southern California. The two subspecies can be separated as follows:

A. Large individuals (12 to 14 mm.) of a rather dull, light metallic blue color; pile over entire body white and extremely dense on thorax, often obscuring the mesonotal coloration, that on the abdomen very appressed. (Known only from Riverside and San Bernardino counties in southern California) .....
E. smaragdinus pilosus Schlinger, n. subsp.

B. Smaller individuals (8 to 12 mm.) of a bright metallic green, blue, or purple color; pile over entire body golden yellow or yellowish-white (rarely with brown tint) which usually does not obscure the mesonotal coloration. (Distributed from Clear Lake, northern California, to 27 mi. south of San Vicente, Baja California, Mexico)
E. smaragdinus smaragdinus Gerstaecker

Eulonchus smaragdinus smaragdinus Gerstaecker, new status

(Figure 1)

Eulonchus smaragdinus Gerstaecker 1856, Stettin. Ent. Zeit. 17: 360–1; Melander 1902, Ent. News 13: 181; Cole 1919, Trans. Amer. Ent. Soc. 45: 32–34, pl. 4, fig. 16 (not specimens from San Bernardino County, California); Sabrosky 1948, Amer. Midland Nat., 39: 388–9; Schlinger 1952, Pan-Pacific Ent. 28: 220.

Type data.—One of the two cotype specimens of *E. smaragdinus* was examined by the author (1952) and designated as a lectotype. This specimen, a male, and the other cotype male specimen are in the Zoologisches Museum Collection in Berlin.

This subspecies appears to be sympatric with *E. smaragdinus pilosus* as far as area is concerned; yet both subspecies have never been collected together in the identical locality or on the same day. If they should be found to be completely sympatric, then perhaps these forms could be considered sibling species. The differences cited above in the key should suffice to distinguish the two forms in any event.

Distribution.—The complete distribution of the species is expressed by this subspecies, and ranges from Lake County in northern California to 27 mi. S. San Vicente, Baja California, Mexico.

Specimens examined.—(345), 288 ♂♂, 57 ♀♀. Specimens were seen from the following localities in California: ALAMEDA COUNTY: Oakland and Diamond Canyon. CONTRA COSTA COUNTY: Berkeley and Mt. Diablo. EL DORADO COUNTY: Strawberry. INYO COUNTY: Whitney Portal and Mt. Whitney. LAKE COUNTY: Lakeport and Clear Lake. LOS ANGELES COUNTY: Fish Canyon, Crystal Lake, Beverly Glen, Westwood Hills, San Gabriel Mts., Monrovia Canyon, Camp Baldy, Santa Monica, and Tanbark Flat. MARIN COUNTY: Fairfax, Mill Valley, Mt. Tamalpais, Tamalpais. MONO COUNTY: Sardine Creek. MONTEREY COUNTY: Carmel, Pacific Grove, Paraiso Springs, Pebble Beach, Monterey, Bixby Creek and Arroyo Seco Camp. NAPA COUNTY: Samuel Springs. ORANGE COUNTY: Laguna Beach and Laguna Mts. PLACER COUNTY: Cisco and Emigrant Gap. RIVERSIDE COUNTY: Idyllwild, Herkey Creek, Riverside, Ribbonwood, The Gavilan and Perris. SAN BERNARDINO COUNTY: Seven Oaks, Claremont, Cucamonga Canyon, Bear Valley, Sheep Canyon, Forest Home, San Antonio Canyon and Cobil Canyon. SAN DIEGO COUNTY: Pine Canyon. SAN FRANCISCO COUNTY: San Francisco (sand dunes) and Lone Mountain. SAN LUIS OBISPO COUNTY: San Luis Obispo and

Morro Bay. SANTA BARBARA COUNTY: Lompoc. SANTA CLARA COUNTY: Los Gatos, San Antonio Valley and Mt. Madonna. SANTA CRUZ COUNTY: Mt. Herman, Highland District and Glenwood. SOLANO COUNTY: Green Valley. SONOMA COUNTY: Glen Ellen and Sobre Vista. TULARE COUNTY: GIANT FOREST, Sequoia Nat. Park. TUOLUMNE COUNTY: Strawberry. Some of these specimens were collected on flowers of *Circium, Clarkia, Delphinium, Diplacus, Pentstemon* or *Salvia*.

I have also examined 2 ♂♂, 27 mi. S. San Vicente, Baja California, MEXICO, collected by R. L. Langston on April 25, 1950. These are the only specimens known to me from outside California.

Flight Periods.—♂♂ April 25 to July 9; ♀♀ May 7 to July 27. Two interesting unincluded records are: 2 ♂♂, Seven Oaks, San Bernardino County, California, October 15, 1934, collected by A. C. Browne and 1 ♂, Monterey, Redwood Forest, California, September 18, 1951, collected by W. K. Dayton. To my knowledge these are the latest collection records for any species of *Eulonchus*; however, since they appear to be very atypical records, they were not included in the normal flight range period given above. Further verification of these late occurrences seems desirable.

Discussion.—Cole (1919) noted some of the variation found in this subspecies, and Sabrosky (1948) discussed this subspecies at length and noted these two important features: First, that the frontal triangle "is smooth, highly polished and glabrous, and the linear oral margin has no long hairs but only a thick-set fringe of minute pale hairs." This feature is evident, also, in *E. halli* and it therefore becomes a character of the *smaragdinus* group. Secondly, he noted sexual dimorphism in the structure of the antennae, and was the first to point out that the apices of the antennae of both sexes contained several minute setae.

Eulonchus smaragdinus pilosus Schlinger, new subspecies

Eulonchus smaragdinus (not Gerstaecker 1856, Stettin. Ent. Zeit. 17: 360); Howard 1901, The Insect Book, p. 134, pl. 18, fig. 23; Cole 1919, Trans. Amer. Ent. Soc. 45: 33–34 (only the specimens from San Bernardino County, California).

This subspecies differs from the nominate form in its larger size, light-brown antennae, metallic greenish-brown coxae, dull metallic blue abdominal coloration, thoracic pile white and more dense, very shaggy on pleura, and in the abdominal pile being more appressed and forming wider posterior tergal bands on each segment. Also, the distribution of this subspecies appears locally distinct from the nominate form. The female is unknown.

Holotype and paratopotype male.—San Bernardino County, California, collected by D. W. Coquillett in the 1890's; there are also two male paratypes from Riverside County, California as follows: 1 ♂, Banning, May 30, 1928 (E. C. Van Dyke) and 1 ♂, San Gorgonio Pass, May 28, 1941 (E. C. Van Dyke). The holotype and paratopotype will be deposited in the USNM collection, one paratype in the CAS collection, and one paratype in the author's collection.

Discussion.—The holotype male was the specimen figured by Howard (1901), and the specimen bears the label "Insect Book Pl. 18, fig. 23," which corresponds to Howard's figure. Other than the absence of the left hind tarsus the specimen is in perfect condition.

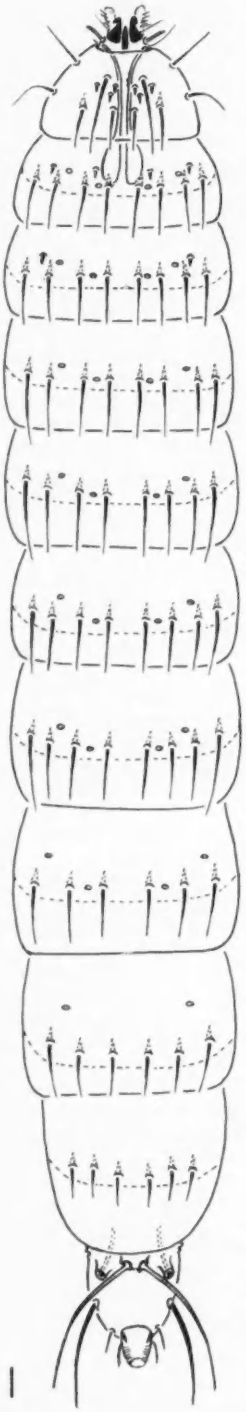
Although *E. s. pilosus* is known from only four male specimens, all of these individuals are quite similar in appearance. They offer no characteristics that confuse this population with that of the nominate form. An examination of the paratype male genitalia showed no essential differences from that of the nominate form.

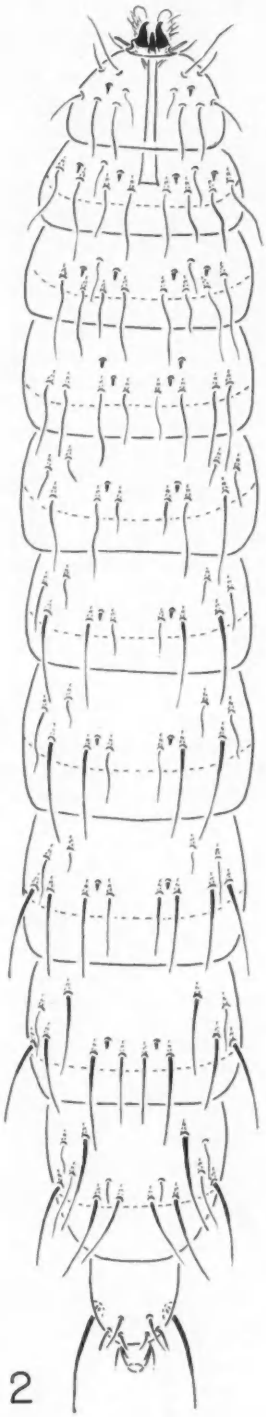
Eulonchus halli Schlinger, new species

(Figure 2 and Plate 1)

Male.—Length of entire specimen 10 mm., wing length 8.5 mm. *Color* dark metallic greenish-purple except for dark brown terminal antennal segment, wing veins, narrow rim of squama, distitarsi, base of claws, tibial spurs, halter base, coxae, and basoventral area of proboscis; eyes, ocellar tubercle, basal antennal segments, and most of remainder of legs black; apex of femora, halter knob, pulvilli, and maxillary palpus, whitish-brown. *Pile* white, quite dense on eyes reaching out as far as apex of antennal segment II, that of occiput above reaching beyond apex of ocellar tubercle, that on thorax and coxae thick, shaggy, about as long as mid-basitarsis, somewhat longer and thicker anteriorly, that on squama thick but shorter than on thorax, that on femora and abdomen not thick enough to obscure ground color, about one-half as long as on thorax, somewhat longer on tergite I and sternites I and II, that on tibiae short, that on tarsi shorter and with slight golden reflections.

Head.—Antenna about three-fourths head height in length, segment III nearly parallel-sided, truncate at apex (without apical setae), whitish-pollinose at joint between II and III; sensorial pits three, two parallel to each other near inner base of segment III, the other slightly farther out; ocellar tubercle high, bifurcate, without median projection; lateral ocellus large, median ocellus small and hidden below anterior base of bifurcation; maxillary palpus about as long as ocellar tubercle, with five to six long apical hairs; proboscis short, not reaching beyond abdominal segment III, distinctly curved upwards, heavily ridged ring-like from base of prementum to labellum; labellum short, rounded at apex, about one-half as long as anteclypeus.





FIGS. 1 and 2.—Aedeagi in lateral view.

FIG. 1, *Eulonchus smaragdinus* Gerstaecker (San Francisco, California).

FIG. 2, *Eulonchus halli* Schlinger (Riverside, California, holotype).

Thorax.—Legs short for *Eulonchus* species, particularly middle tarsus, hind femur distinctly enlarged at apex, tibial spur on each leg well developed, acute, about as long as antennal segments I and II combined; squama opaque white; wing hyaline, wing shape and venation similar to *E. smaragdinus*, but wing somewhat more narrowed; posterior cells complete.

Abdomen.—Short, not much longer than wide, widest at segments II and III, intersegmental membrane of a dirty white color; genitalia formed nearly as in *E. smaragdinus*, but aedeagus shorter and of a different shape (fig. 2); basistylus more robust and dististylus shorter.

Female.—As described for male except head somewhat smaller, wing and legs somewhat longer; antennal segment III sharply acuminate, tapering evenly from base to apex; ocellar tubercle slightly higher; genitalia as in *E. smaragdinus* female.

Paratype variation.—Some of the male paratypes are larger than the holotype, but most range between 9 and 12 mm. in length. The female paratypes fall within the male size range. A few of the male paratypes have distinct bluish or greenish reflections on their abdomens, and one male paratype had a nearly straight proboscis.

Egg.—Small (0.50 mm. long, 0.25 mm. wide) dull black, pear-shaped in outline, flat, and finely reticulate throughout.

First-instar larva.—Minute (1 mm. long, 0.15 mm. wide) planidium with small mandibulate head and 11 body segments, each segment except head bearing several small and large setae of various types. The head contains a pair of heavily sclerotized, upturned mandibles, small, simple antennae, a minute lateral seta, and a strong, buccopharyngeal armature. The caudal segment contains a pair of dorsal spiracles, a pair of long dorsal and lateral setae, a terminal suction disc, and several pairs of short setae (see plate 1).

Holotype male.—Riverside, California, March 7, 1934 (P. H. Timberlake, CAS), feeding at flowers of *Cryptantha intermedia* Greene. The genitalia (No. 51–3–1d) are mounted on a slide. One antenna has been dissected and is mounted on a point with the specimen.

Paratopotypes.—32 specimens (26 ♂♂ and 6 ♀♀). 4 ♂♂, 2 ♀♀, March 21, 1929, April 3, 1929, March 29, 1936, March 25, 1941, April 3, 1946, April 19, 1953 (P. H. Timberlake, EIS, BCC) feeding at flowers of *Cryptantha intermedia* Greene and *Lantana* species; 6 ♂♂, April 4, 1954, March 26, 1956 (J. C. Hall, EIS); 2 ♂, April 4 and 17, 1937 (G. C. Varley, BMNH); 5 ♂♂, 1 ♀, March 24 and 27, 1957 (E. I Schlinger, EIS); 8 ♂♂, 1 ♀, March 8, 1958 (J. C. Hall, E. I. Schlinger, R. van den Bosch, EIS); 1 ♂, 2 ♀♀, April 9, 1958 (E. I. Schlinger, EIS) all feeding at flowers of *Cryptantha intermedia* Greene.

Paratypes.—39 specimens (30 ♂♂ and 9 ♀♀). 1 ♂, 1.5 mi. N. Perris, Riverside County, California, April 1, 1938 (P. H. Timberlake, BCC); 3 ♂♂, 1 ♀, 5 mi. S. Riverside, California, April 4, 1954 (D. W. Ricker, EIS); 2 ♂♂, 2 ♀♀, same locality, April 9, 1954 (J. C. Hall, EIS); 24 ♂♂, 6 ♀♀, 8 mi. E. Sunnymead, Riverside County, California, March 26, 1958, April 12 and 22, 1958, March 27 and 28, 1959 (J. C. Hall, H. R. Moffitt, E. I. Schlinger, EIS), all feeding at flowers of *C. intermedia* except for one specimen found trying to feed at flowers of *Salvia mellifera* Greene.

I have also examined a male specimen which appears to be a blue color form of *halli* from Baja California, Mexico. It has the data, Valle de la Trinidad, March 16, 1916 (C. F. Harbison, EIS).

Flight periods. ♂♂ March 7 to April 22, ♀♀ March 8 to April 12. This is the first species of *Eulonchus* to appear in the spring, and according to the records above, has disappeared from the scene when other *Eulonchus* species are abundant in June and July.

The holotype will be deposited in the CAS collection and paratypes will be deposited in the AMNH, BCC, BMNH, CAS, CIS, DEI, EIS, and USNM collections.

Discussion.—This distinctive species is closely related to *E. smaragdinus*, from which it can be differentiated by its shorter proboscis, shorter labellum, bifurcate ocellar tubercle, shorter legs, general coloration, and by the male genitalia.

E. halli is apparently sympatric with *E. smaragdinus* in southern California and Baja California, yet there is a definite temporal separation of these species (see recorded data above), since both species have never been collected together in the same place at the same time. This is probably due to the occurrence and development of their specific hosts.

Apparently the association of *E. halli* and the plant *Cryptantha intermedia* Greene represents a case of mutualism. This is the first case I am aware of concerning a plant-acrocerid relationship that appears to be specific. The short proboscis of *E. halli* is well adapted to be inserted into the short corolla of *C. intermedia*, and during the years 1957 to 1959, the author was able to collect and observe these flies in some abundance. In all cases this species of *Eulonchus* was collected on or between individuals of this plant species, even though such plants as *Amsinckia douglasiana* DC, *Brodiaea* sp., *Encelia actoni* Elmer, *Eriogonum fasciculatum* Benth, *Gilia* sp., *Mirabilis laevis* (Benth.) Curran, *Pentstemon* sp., *Plagiobothrys* sp., and *Salvia mellifera* Greene were in bloom nearby. Males were commonly collected while flying from one plant of *C. intermedia* to another, apparently in search of females. The females seemed to feed more and were most often collected while feeding on the nectar of this plant. Judging from my observations on the flight and feeding habits of these flies, and from the considerable amount of pollen found on the mouth

parts, legs, and particularly among the long pile around the flies' occiputs, it is concluded that a large share of the pollination of *C. intermedia* is attributable to *E. halli*. In exchange for pollinating this species of plant, *E. halli* obtains the necessary nectar to expedite its rapid flight habits. The fact that the most prolific blooming period of *C. intermedia* (March to April) coincides with the occurrence of *E. halli* in Riverside, California, adds considerable weight to this mutualism theory.

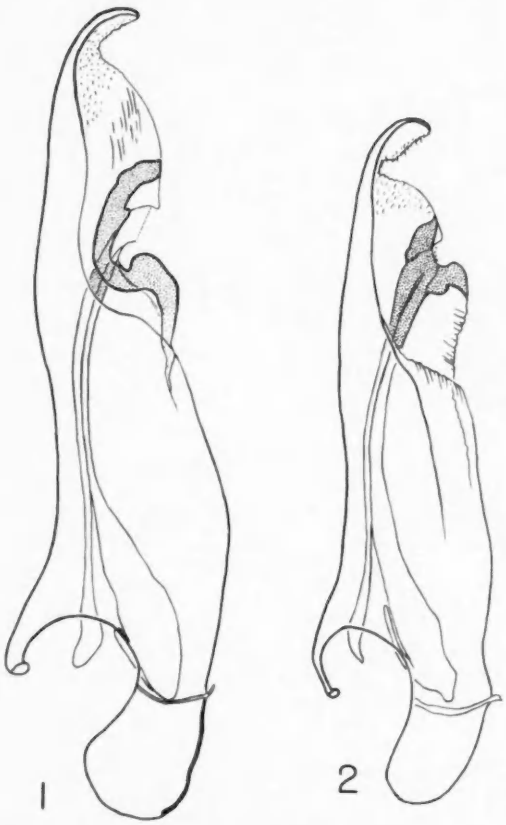


PLATE 1.—First-instar larvae of *Eulonchus halli* Schlinger. FIG. 1, dorsal view. FIG. 2, ventral view.

There are also several species of bees which pollinate *C. intermedia* in the Riverside area, and although I have been unable to determine whether the bees or *E. halli* are the better pollinators, it would seem that due to its rapid flight and quick feeding habit an individual fly may be responsible for pollinating as many flowers as does an individual bee. I might add that because of the extremely rapid flight patterns of *E. halli*, many more flies were observed than were collected, and it was not uncommon to see or to hear the high-pitched tone of 50 or more flies while trying to collect three or four in my net.

One female of *E. halli* (collected by J. C. Hall in Riverside on April 9, 1954) laid nearly 100 eggs in a gallon jar on April 10. First-instar larvae emerged on April 17, and the figure of the larva (pl. 1) was made from one of these larvae.

It gives me great pleasure to name this species after one of its collectors and my associate, Jack C. Hall of the Department of Biological Control, University of California, Riverside.

ACKNOWLEDGMENTS

I would like to extend my sincere thanks to all persons and institutions involved in the loan of specimens for this study. Due to the fact that 29 collections were utilized for this study, a complete list of the people, institutions, and abbreviations for the latter is given here with the hope that this list of acknowledgments will suffice for this and future parts to be published on the genus *Eulonchus*.

(ALM) Axel L. Melander, Riverside California; (AMNH) American Museum of Natural History, New York, New York (M. A. Cazier and C. H. Curran); (BCC) University of California, Department of Biological Control, Riverside (P. H. Timberlake); (BMNH) British Museum of Natural History, London, England (H. Oldroyd); (CAM) Colorado Agricultural and Mechanical College, Fort Collins (T. O. Thatcher); (CAS) California Academy of Sciences, San Francisco (E. L. Kessel, E. S. Ross); (CHM) Charles H. Martin, Corvallis, Oregon; (CIS) California Insect Survey, University of California, Berkeley (F. R. Cole, P. D. Hurd, Jr.); (CSD) California State Department of Agriculture, Sacramento (H. H. Keifer); (CU) Cornell University, Ithaca, New York (H. Dietrich); (DEI) Deutsche Entomologische Institut, Berlin, Germany (W. Hennig); (DEJ) D. Elmer Johnson, Dugway, Utah; (EIS) Evert I. Schlinger, Riverside, California; (GEB) George E. Bohart, Logan, Utah, now at (CAS); (LAM) Los Angeles County Museum, California (W. D. Pierce); (MCZ) Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (J. Bequaert and P. J. Darlington, Jr.); (OSC) Oregon State College, Corvallis (F. F. Hasbrouck and V. Roth); (PANS) Philadelphia Academy of Natural Sciences, Pennsylvania (J. A. G. Rehn); (SDNHM) San Diego Natural History Museum, California (C. F. Harbison); (UCD) University of California at Davis (A. T. McClay); (UCLA) University of California at Los Angeles (W. A. McDonald); (UI) University of Idaho, Moscow (W. F. Barr); (UK) University of Kansas, Lawrence (R. H. Beamer); (USAC) Utah State Agricultural College, Logan (F. G. Knowlton); (USNM) United States National Museum, Washington, D. C. (C. W. Sabrosky); (UU) University of Utah, Salt Lake City (G. F. Edmunds, Jr.); (WSC) Washington State College,

Pullman (M. T. James); and (ZI) Zoologische Institut, Berlin, Germany (F. Peus).

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THE COLORS OF DESERT WATER BEETLES--ENVIRONMENTAL EFFECT OR PROTECTIVE COLORATION?[1]

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ABSTRACT

The best explanation for the preponderance of brightly colored and distinctly patterned water beetles in the desert regions of the southwestern United States and northern Mexico is that such coloration and marking is disruptive and helps conceal the beetles from predators in the desert streams and pools. The colors and patterns have undoubtedly developed as the effect of random gene mutations acted upon by natural selection. Some mutations producing lighter patterns may still be in a condition of balanced polymorphism with the original dark pattern genes. There is little evidence for environmental production of the light colors and patterns, and none for the genetic fixation of originally environmentally produced, nonadaptive modifications.

Water beetles of the families Dytiscidae and Hydrophilidae are so commonly dark brown or black that brightly colored or marked species are exceptional and attract immediate attention. In northern latitudes, lightly colored or conspicuously striped, spotted, or mottled forms are usually associated with streams or the margins of lakes. For example, on Southampton Island in the Canadian Arctic, the only species with conspicuous color patterns are *Hydroporus lapponum* Gyll., found along the edges of tundra lakes, and *Oreodytes* sp. cf. *scitulus* LeC. in streams. The species found in peat pools or situations with vegetation are almost uniformly brown or black (Young 1960). Similarly, the dytiscids which inhabit the beautifully clear trout ponds and streams of the White Mountains are the brightly colored species of *Hydroporus*. The inhabitants of the bogs and vegetated ponds in the same areas are mostly dark, somber beetles usually without any conspicuous color pattern.

Correlations of this sort between habitat and coloration have been observed in water beetles in many parts of the world (cf. Guignot 1933). Nowhere, however, are brightly colored and marked species more frequent than in the Sonoran desert region and generally over our Southwest and the deserts of Northern Mexico. Here a large proportion of the water beetles are marked with yellow, orange, or other colors in stripes, spots, or dashes in contrast to their dull relatives in the same genera elsewhere. Some of the particularly brightly colored and marked Sonoran species are: *Thermonectus marmoratus* Hope, *Laccophilus insignis* Sharp, *L. pictus* Castelnau, *L. coccinelloides* Régimbart, and *Suphisellus mexicanus* (Sharp). There are also many brightly marked species of the genera *Desmopachria*, *Oreodytes*, *Deronectes*, *Bidessus* (*sensu latus*),

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Berosus, and others. There are even some conspicuously marked species of *Rhantus* and *Cybister*, the species of which are normally very dark.

In the deserts and semidesert areas, the brightly marked forms are not strictly confined to streams but also occur in the desert ponds, marshes, and flats sometimes many miles from permanent water. Nearly all of them are adapted to living in unstable situations which are seasonal or fluctuate greatly. The vagility of all the desert species is very high, and some species have extended their ranges over vast areas. For example, *Eretes sticticus* (Linn.) was originally an Old World form, but it is now widely distributed in the Antillean-Carribean region.

Some brightly marked Sonoran species extend into the eastern United States where their coloration is especially conspicuous in contrast to that of the old Appalachian woodland fauna. In the more humid regions, such as peninsular Florida, the colors of these western forms is often subdued by a diffuse melanism which mixes with or covers the lighter pigments.[2] This seems to be a secondary melanization which can only be detected against the background of a lightened color pattern.

In the Mexican desert region and adjacent portions of the United States, contrastingly dark water beetles occur in mountain streams and pools. The dark coloration of these is presumably due to a primary melanization representing the primitive condition. In the Sierra del Tigre range in Sonora and the Chiricahuas and Huachuchas in Arizona, for example, the brightly colored forms of the desert flats and lower hills are replaced at higher elevations by black or brown species such as *Hydroporus kingi* Clark, *Deronectes aequinoctialis* Clark, *D. striatellus* LeC., *Agabus lugens* LeC., and the large *Rhantus atricolor* Aubé. Some species of *Deronectes* and *Bidessus* have smaller, darker forms in the mountains and larger, lighter ones in the adjacent deserts and foothills.

The presence of so many uniquely marked water beetles in one region cannot be pure coincidence. The first theory that comes to mind is that the colors and patterns are the direct effect of the extremely dry, hot climate. The Sonoran species correspond roughly to Gloger's rule (hypothesized for birds and mammals) in that the dark melanins seem to be replaced by similar compounds of red, yellow, or orange color (Dobzhansky 1951, et al.). The melanins of insects are probably not the same as those of vertebrates, however, and there seems to be relatively little evidence for the direct influence of environment except that low temperatures increase melanin formation (Kaestner 1931, et. al.). This may be a partial explanation of the darker forms found at high elevations.

On the other hand, there is abundant evidence for the genetic control of light versus dark patterns in insects. Dobzhansky (1933) and others have also pointed out the greater frequency of genes controlling dark patterns in coccinellid beetles in humid-cold regions and the conversely greater frequency of genes controlling light patters in hot-dry areas. Kalmus (1945) has shown that low humidity and high temperatures favor the survival of the normal *Drosophila melanogaster* over the ebony mutant. Humidity was less effective in this respect, however, than temperature, and the heterozygotes in all cases were superior to either homozygote. It seems possible that the occurrence of light colored forms in hot-dry climates and dark forms in humid regions may be initially conditioned by some physiological advantage inherent in the metabolic processes involved, and the widespread occurrence of melanism in insects in humid areas may indicate that some selection is going on at this level.

An environmental effect cannot, however, be hypothesized for the light colored, brightly marked forms in streams and lakes of northern regions. Humidity and temperature obviously do not coincide to the distribution in all areas, although the changes in pigmentation and color patterns are basically similar. There is, however, one very striking similarity in the habitats of all the light colored, brightly marked forms wherever they are found. That is, they occur in clear water and usually over bottoms which are relatively light in color and free of dense rooted vegetation. Under such conditions, there is simply no place to hide, and any brown or black insect would be conspicuous in the daytime. Spots, stripes, light dashes, or a mottled appearance serve as disruptive coloration, breaking up the outline against the bottom and presumably make the beetles less conspicuous to predators.

Fish and other animals probably prey upon water beetles more than the remains found in stomach analyses indicate. In the case of fish the poor representation of beetles in their food is possibly due to the fact that large fish are usually used for analysis. These generally feed out from shore where beetles are scarce. Birds, including ducks and others, definitely feed upon water beetles along the shores of both streams and standing water. Some years ago, Dr. William H. Coil of Ohio State University sent me specimens of *Bidessus spretus* and *B. obtusus* Sharp which he found in the intestine of a spotted sandpiper from Oaxaca, Mexico. Both of these little dytiscids are brightly marked for the genus, but the conditions under which the sandpiper was feeding were not recorded so that the failure of the protective coloration is not certain.

[2]This melanization does not seem to be involved in the basic hardening and coloring of the cuticle because it is easily removed by dilute hydrogen peroxide. Only prolonged soaking in concentrated peroxide will affect the spots or stripes of the basic patterns.

Under some conditions in the deserts, water beetles are exposed to very intensive predation. During the dry seasons, pools in streams may be so reduced that they literally teem with beetles. I have never actually seen birds feeding on these concentrations, but no shore bird would have any difficulty in making a meal of dytiscids, haliplids, noterids, and hydrophilids. In such circumstances, any mutant which rendered its carrier less conspicuous ought to survive differentially.

During periods when streams are normal, and in the lower mountains where they may be permanent, the brightly colored and marked beetles must be at a definite advantage against the light gravelly, sandy, or silty bottoms. They are certainly protected to a considerable degree from human observation. My first encounter with a living Mexican water beetle was in a tiny spring-fed stream in Nuevo Leon. The crystal clear water was so obviously barren that I had given up collecting in despair and sat idly gazing into a pool when suddenly I realized that the little golden flecks among the pebbles on the bottom were the yellow spots on the elytra of *Laccophilus insignis*. I caught over 20 specimens in that tiny pool in a few minutes once the pattern was recognized.

In other areas of Mexico and the southwestern United States, I have repeatedly observed brightly marked species of *Oreodytes*, *Bidessus*, *Thermonectus*, *Laccophilus* and other genera resting immobile on the bottom along the margins of streams and pools. Quite often they were indistinguishable from the bottom until they moved. Most of the species observed are very active at night when they may spread out away from the margins into deeper water.

Tropisternus mexicanus mexicanus (Castelnau) is another form frequently observed resting on sand or gravel along streams or pools, apparently trusting its coloration to hide it during the day. In this case the protective nature of the conspicuous stripes and blotches may be emphasized by the occurrence of a very dark subspecies (*viridis*)[3] in the dark bottomed situations in peninsular Florida, and an intermediate (*striolatus*) over the rest of the eastern United States (Young and Spangler 1956).

It still seems peculiar that genetically based light patterns should be more frequent in areas of lower humidity and higher temperatures and darker patterns more frequent in regions of high humidity and lower temperatures (humidity being more important than temperature in regard to the latter). It should be emphasized, however, that the correlations are not absolute, and may be in part fortuitous. It has not been shown that either humidity or temperature directly change the basic color pattern of a beetle. In fact, indirect evidence from studies on *Tropisternus* and other aquatic beetles suggests that the basic pattern is not modified even in humid regions where a diffuse melanization, presumably environmental, makes the beetles appear very dark. The pattern of lines and spots remains distinct from the diffuse melanization in the most extreme cases observed (specimens of *Tropisternus collaris* (Fabr.) from central Brazil; cf. Sharp 1883).

In the case of the reduction of dark pigments and the extension of lightly pigmented areas or the suffusion of areas with different pigments, the evidence for environmental control seems to be based largely on general correlations such as the abundance of light-colored forms in dry regions. In the Sonoran deserts, at least, the majority of brightly colored terrestrial insects prove to be either warningly colored or mimetic. Environment may have originally favored light pigmentation in these insects, but this is now maintained by quite different selective forces.

Also opposed to the theory of the environmental production of light colors in the water beetles is the fact that some Sonoran species are dimorphic. For example, *Rhantus mexicanus* Castelnau has a light mottled form and a form with black elytra. The two occur together frequently in the same pools and ponds, and probably represent simple genetic differences. The dimorphism may be maintained as a balanced polymorphism by selection due to predation in the desert-mountain habitats over which the species ranges. Certainly, the black versus light color in this species does not seem to be directly influenced by humidity and temperature.

There are other cases opposed to the general condition which seem to rule out direct environmental influence. In the genus *Hydrocanthus*, a species or series of species form a cline from central Mexico to Maine. In central Mexico the forms are black, in northeastern Mexico and the southern and central U. S. they have black elytra only, while in the northern states they are uniformly reddish brown. An isolated form in the peninsula of Florida is an exception in being as black as the central Mexican form. The black forms here do occur in humid regions, but humidity-temperature correlation seems to break down elsewhere.

The failure of environmental influences in reducing pigmentation, is especially evident in the aquatic family Gyrinidae. The Sonoran species are as uniformly black or greenish as they are anywhere. Certainly they do not show bright patterns. This is correlated with the fact that beetles of this family live on the surface of the water, and disruptive coloration could be of no conceivable utility to them.

We are, of course, not certain that change in the pigmentation in desert areas does not confer

[3]The darkening of this form is due to an extension of the elements of the basic color pattern, and diffuse melanization is minor.

an advantage upon the beetles. The general metabolism is certainly deeply involved in pigment formation. Light pigments in contrast to dark may even be protective against the intense rays of the sun in shallow water or during the periods when migration from one habitat to another becomes necessary. There is evidence from the study of regional melanism, for example in the industrial melanism in the Midlands of England, that the melanic condition in some cases is associated with greater viability, etc. Similar advantages may accrue in the reverse condition in another environment. The preponderance of evidence, however, indicates that melanism is adaptive in the sense that it protects the organisms possessing it from predators in the habitat in which they normally occur, be it the smutty woods of the Midlands or the primitive Caledonian forest (Kettlewell 1958). The same conclusion, I feel, will eventually be reached concerning the Sonoran water beetles, and many light colored, brightly marked aquatic forms from other regions.

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THE BIOLOGY OF HETEROSTYLUM ROBUSTUM (DIPTERA: BOMBYLIIDAE), A PARASITE OF THE ALKALI BEE[1]

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ABSTRACT

Heterostylum robustum (Osten Sacken) is the principal parasite of the alkali bee (*Nomia melanderi* Ckll.) in the Northwestern States. It also parasitizes other species of *Nomia* and at least one species of both *Nomadopsis* and *Halictus*. It ejects eggs into and near the nest mounds of its host, but does not readily discriminate between nest burrows and other depressions in the ground. The first-instar larva finds its way to a host larval cell, where it waits until the host larva is full grown before feeding on it. The parasite larva passes through four instars, progressing from a slender, active first instar through a very brief second instar, and a soft, helpless third instar, to a tough, more active fourth instar. Some larvae apparently mature on a single host, but others partially drain the fluids from a second as well. In the late summer or fall the mature larva makes an overwintering cell in the upper few inches of soil. It pupates in the late spring, and shortly before ecdysis bores to the ground surface. The adult emerges as soon as the pupa thrusts its head and thorax clear of the surface. Mating usually takes place on vegetation surrounding the host nesting site.

As the principal parasite of the alkali bee (*Nomia melanderi* Ckll.) over much of its range, *Heterostylum robustum* (Osten Sacken) is an important economic insect. The alkali bee is an excellent alfalfa pollinator, chiefly responsible for the high yields in the major seed-growing areas of Washington, Oregon, Idaho, and Wyoming. In some areas where alkali bees were formerly abundant, *robustum* now holds their population to an insignificant level. The percentages of host prepupae destroyed vary from over 90 in nesting sites of Cache Valley, Utah, to 5 or less in some sites near Wapato, Washington. In many areas 20 to 40 percent of the host larvae are destroyed. In Oregon a nesting aggregation of over half a million bees in 1955 had an incidence of 91 percent parasitism in 1956. In 1957 the aggregation was only half as large, but parasitism

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[3]Oregon State College, Corvallis.

fell to 50 percent. In 1958 parasitism was 30 percent and the bee population appeared to be nearly stabilized.

FIG. 1.—Adult female *Heterostylum robustum* ovipositing over nest entrance of *Nomia melanderi*.

Before 1946 there were several alkali bee nesting sites west of Logan, Utah, each containing over 100,000 nests. Bees from these sites were responsible for some excellent seed yields in neighboring fields. Todd (1946) described the ground on these sites as covered by thousands of empty bombylliid pupal skins. For the next 10 years parasitism in the Logan area was extremely high and alkali bee populations were too small to benefit the farmers appreciably. Since 1956 a slight reversal of this downward trend has been observed. It may have been the result of parasite control measures attempted on an experimental basis. However, another important dipterous parasite in this area, ***Euphytomima nomiavora*** James, was controlled by the same measures, so that the benefit cannot be ascribed solely to bee fly control.

Apparently two factors have been responsible for the failure of the bombyliid parasite to wipe out its host completely in the Logan area. Each year a few of the bees nest in a solitary fashion and thus avoid the heavy attack suffered by the more gregarious individuals. Furthermore, some of the late-emerging bees continue to lay eggs after most of the parasites have disappeared and a partial second generation appears in late August after all the flies have disappeared. The first alkali bees to emerge each summer concentrate their nests in the most nearly ideal portions of the nesting sites. Consequently, several hundred to a thousand or more nests appear in these favored areas in spite of an annual parasitism of well over 90 percent.

DISTRIBUTION AND HOST RANGE

The recorded geographic range of ***Heterostylum robustum*** includes the Pacific and Rocky Mountain States as well as the southern Great Plains, the lower Mississippi Valley, and Florida (Painter 1930, 1958). In the Western States it is found primarily in the larger valleys. Since its range greatly exceeds that of *Nomia melanderi*, it must successfully parasitize other species of bees. Frick (1958) stated that he has seen a specimen of ***robustum*** from Colorado labeled as a parasite of *Nomia bakeri* Ckll. In the vicinity of Logan it has been seen to deposit eggs in the nests of several species of solitary ground-nesting bees in and near the nesting sites of alkali bees. The larvae have been observed developing normally in the cells of *Nomia triangulifera* Vachal and *Nomadopsis anthidius* Fowler. Early stages of the larvae have also been found feeding on prepupae of *Nomadopsis scutellaris* Fowler, a small species that nests in alkali bee sites, but full-grown larvae and pupae have not been found in strict association with this species. The senior author once saw adults laying eggs in a small nesting site of ***Halictus rubicundus*** Christ. Subsequently first- and third-instar larvae, which appeared normal, were seen on the host prepupae.

Although ***robustum*** seems to be an ever-present parasite in alkali bee nesting sites in Washington, Oregon, Idaho, northern Nevada, and northern Utah, it has not been found in Wyoming or central and southern Utah, although a single specimen of ***Heterostylum englehardti*** Painter was seen laying eggs in an alkali bee nesting site in central Utah (near Delta). In the Uintah Basin of eastern Utah a small number of larvae were taken which closely resembled ***robustum***, but certain details observed in their life history were different from those observed for ***robustum*** in other areas.

In northern Utah and in Oregon the adults of ***robustum*** were observed taking nectar from flowers of alfalfa and sweetclover. However, its host-plant range probably includes many other flowers with moderately long corolla tubes. In 1947 it was conspicuously abundant in many alfalfa fields in northern Utah, but was never observed to trip the flowers. It rarely alighted on the flowers, perferring to sip nectar while

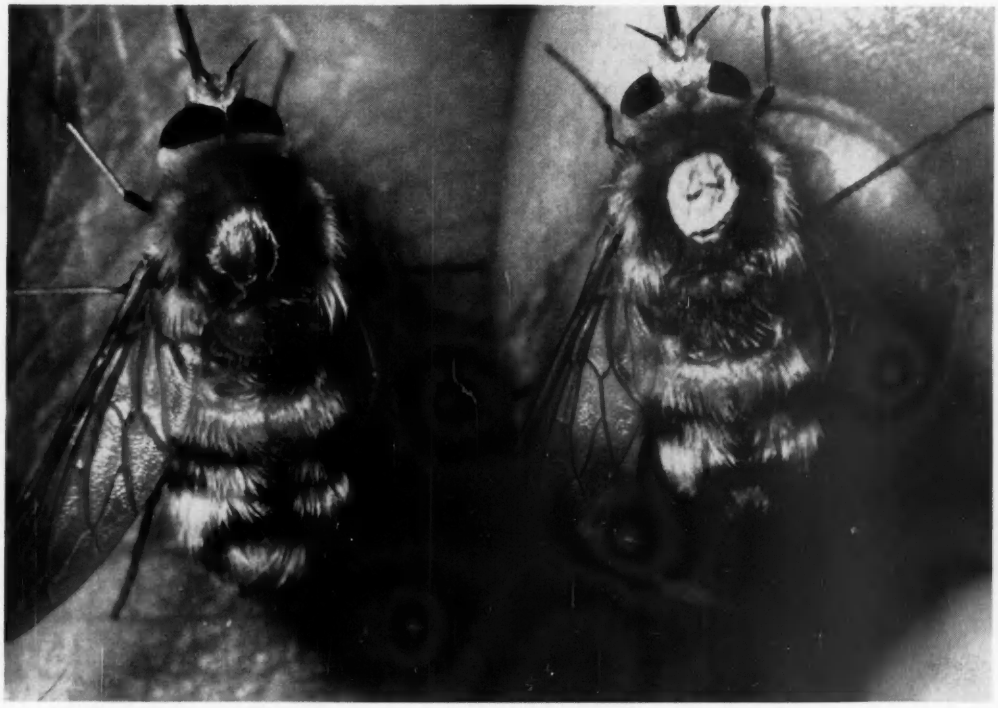

FIG. 2.—Teneral male (left) and female (right) of *Heterostylum robustum*.

hovering directly in front of them. The habit of hovering while taking nectar has also been seen in *Bombylius* but not in *Anthrax*, *Exoprosopa*, and other short-tongued genera of Bombyliidae (Clausen 1940).

ADULTS

The adult (fig. 1) is conspicuous and fascinating as it persistently hovers and dips over alkali bee nests with its wings producing a continuous high-pitched whine. It is a large, robust species (fig. 2)

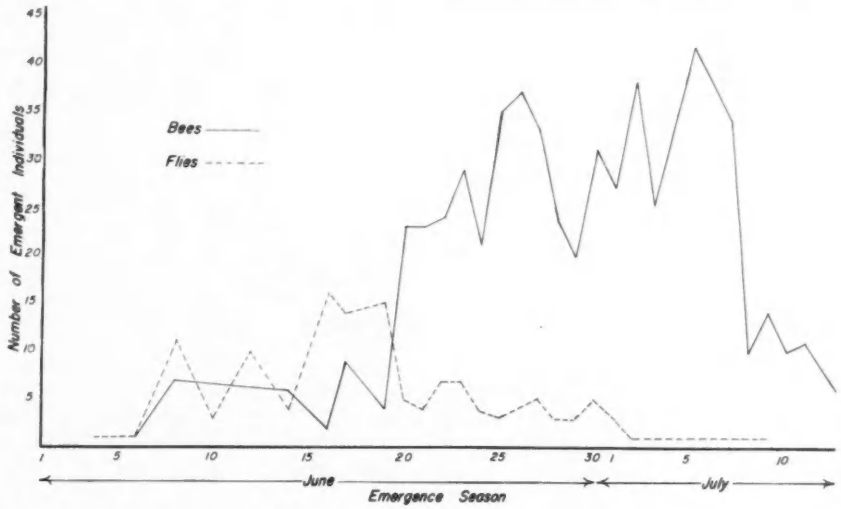

FIG. 3.—Emergence of *Heterostylum robustum* and *Nomia melanderi* in Oregon.

with unclouded wings, tan thorax, a gray, buff, and black pattern on the abdomen, and a long proboscis. With age it loses much of its abdominal hair and becomes nearly uniformly dark gray. The sexes are similar in appearance except that the males are holoptic and the females dichoptic (fig. 2).

FIG. 4.—Eggs of *Heterostylum robustum*.

Emergence.—The first adult bee flies appear a week to 10 days earlier than the alkali bees, but their emergence period overlaps that of their host by several weeks. Emergence usually begins in late June, reaches its peak early in July, and is nearly complete by the middle of July. In any given year the start and peak of bombyliid activity at different alkali bee sites in the same area may vary as much as 2 weeks. In 1956 and 1957 flies began emerging late in June in eastern Oregon and western Idaho, but in 1958 there was an early emergence and the flies appeared a month earlier (fig. 3). Although emergence tapers off rapidly, a few flies continue to emerge for several weeks. There is evidence that these late-emerging flies come from larvae that matured too late in the fall to move up to the normal zone for overwintering. The peak population of adults generally coincides with that of the host, but the host population remains high for several weeks longer.

On warm days emergence begins about 8 a.m. and continues until about 1 p.m., with the peak occurring between 9 and 10. After hardening, the still feeble adults fly to a nectar source and do not begin ovipositing over the nest for at least 2 days.

Oviposition.—The parasites are active over the host nests after the temperature reaches 80° F., which is usually about 9 a.m. They are most abundant shortly before noon, and by about 2 p.m. most of them have taken shelter in surrounding vegetation where they exhibit a marked negative phototropism. In the greenhouse they seek the heaviest shade available.

Even though several hundred flies may emerge from 2 or 3 square yards of soil, rarely are more than one or two adults seen hovering over an area of the same size. Although the rate and

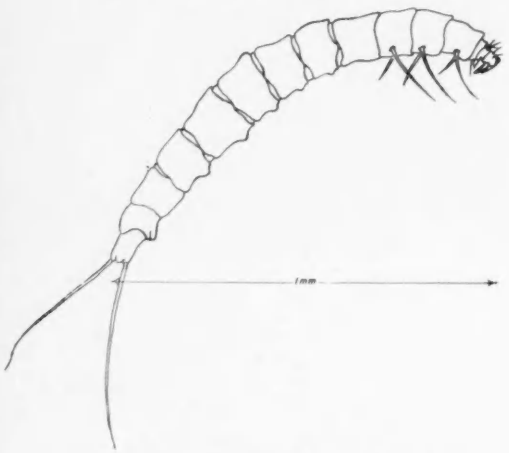

FIG. 5.—First-instar *Heterostylum robustum*.

distance of their dispersal from the point of emergence have not been determined, they must be considerable. On a small, rather isolated alkali bee site in Utah, attempts were made to trace the activities of marked flies. Of 162 individuals marked at the time they emerged in the summer of 1958, only two were seen during numerous subsequent observations. Of 45 marked while ovipositing, only one was seen in subsequent daily observations. Neither mortality nor disturbance caused by marking them appeared to be responsible for their disappearance. Marked individuals continued to oviposit as soon as they were released and in the laboratory they could be kept alive for more than a week.

In Oregon control of the fly was attempted on a small nesting site by scraping off the top layer of soil, killing each fly as it emerged, and swatting all ovipositing flies. In spite of this, nearly equal numbers of flies appeared on the site each day of the active season. Even when blocks of soil

containing alkali bee larvae were moved to an area at least a mile from known sites and all flies emerging from them were killed, flies were numerous once bee activity began. Apparently the parasites not only disperse widely soon after emerging, but continue to shift their operations from one territory to another throughout their life.

The females (fig. 1) spend most of their flying time over the nests, hovering about ¾ inch above the ground with their posterior legs held above their backs. When they perceive a hole or crack

FIG. 6.—*Heterostylum robustum* larva feeding on early pupa of overwintered *Nomia melanderi*.

in the ground, they dip downward about ½ inch, give their abdomen a brisk downward "flick," and touch their hind tarsi to the ground. Apparently the egg is released at this moment. After discharging an egg, the female sometimes hovers again for a second or two and then releases another egg. She may repeat the process five or six times, after which she rises several inches and seeks other holes or cracks a few inches or feet away. *H. robustum* differs from certain other bombyliids in that it never lands during its ovipositing activities. *Bombylius* hovers over the nest mounds of its host, but it frequently lands and appears to lay some of its eggs while on the ground (observed in Utah by the senior author). According to Fabre (1913), *Anthrax* clings to the burrow entrance of *Chalicodoma* bees and lays its eggs by pressing the tip of its abdomen against the soil.

The egg-laying capacity of *robustum* is enormous. One female was observed to make 210 dips in 20 minutes. If she laid an egg each time she dipped, she must have laid at least 1,000 eggs during the day, even allowing for periods of relative inactivity. In Oregon 25 ovipositing females had an average of 169 (range 44 to 424) mature or nearly mature eggs in the lower ovaries and oviducts, and equal or greater numbers of undeveloped ova in the upper portion of the ovaries. Zakhvatkin (1931) states that *Calistoma desertorum*, a species parasitic on grasshopper egg masses, can produce from 1600 to 2000 eggs.

In spite of the rather thin scattering of parasites over the nesting sites, few holes or cracks escape oviposition. In 1955 a series of vials were dipped in black ink and buried flush with the ground surface. Each vial accumulated 50 or more eggs in a single day, indicating that the flies are accurate in their oviposition. However, accurate aim does not seem to be essential. When portions of a nesting site were boxed in with wire screen having a mesh just open enough to permit entry of the bees, the parasites released their eggs over the wire. When soil in the area was examined in the fall, the parasitism under the screens was nearly as great as in surrounding area.

Although the flies seem to be indiscriminate in their choice of depressions for oviposition, they are rarely found over areas where bees are not nesting in abundance. Artificial holes made several yards away from a nesting site are seldom visited. Perhaps the flies are guided to the nesting sites by their sense of smell.

EGGS

The eggs are 1.2 mm. long and 0.7 mm. wide. They are oval and equally tapered at each end. The chorion is smooth and white with pearly, irridescent reflections. The eggs have a mucilaginous coating to which soil particles adhere (fig. 4). When 42 eggs were brought to the laboratory and held at room temperature shortly after being laid, they hatched in 8 to 11 days, the average being 9. Since the incubation period is rather long, the eggs probably have to land in holes or cracks in the ground or in the crowns of plants to avoid lethal exposure to the sun.

LARVAE

The immature stages of the Bombyliidae undergo striking hypermetamorphosis. The various forms of the larvae and the peculiar modifications of the pupae represent obvious adaptations to changes in their mode of life from one stage to the next. The developmental stages of *robustum* are similar to those of other bombyliids, but they differ in several particulars.

First instar.—The first-instar larvae (fig. 5) are slender, planidiaform, about 1.6 mm. long, nearly white, very active, and have a pair of long caudal bristles. The mouth parts, which are large in relation to the body, have a median pair of tong-like hooks flanked by long, slender, maxillae which bear club-shaped palpi tipped with long bristles. The head and neck have eight pairs of bristles, and each thoracic segment has a single

pair. Abdominal segments 2–6 have small, paired pseudopods, and segment 8 has a pair of double pseudopods near the posterior margin. The respiratory system appears to be peripneustic, although the abdominal spiracles anterior to the penultimate ones are poorly developed and may be vestigial.

FIG. 7.—Unfed and fully fed first-instar *Heterostylum robustum* on last-instar *Nomia melanderi*.

The first-instar larvae inch their way along the ground by grasping it with their mouth hooks, flexing their body, making contact with their posterior pseudopods, and then pushing forward. Little is known regarding the activities of the first-instar larvae prior to feeding. They are never found on the host larva until it is in its final instar. Inspection of many cells in earlier stages of host development showed only a few first instars, and they were either inside the pollen ball or on the wall of the cell against the side of the ball. Although the tiny larvae may have been overlooked in the other cells examined, we are inclined to think that they are able to enter the cells through the entrance plug after the cells are sealed. This ability probably explains the occasional appearance in the early summer of ***robustum*** larvae in various stages feeding on overwintered prepupae and pupae (fig. 6). Early in the season the parasites probably eject many of their eggs into reopened burrows of the preceding season, and some of the first instars invade the cells of hosts that are late in breaking winter diapause.

If the parasite survives for long periods in the soil before invading a cell in which the host is a full-grown larva or prepupa, intensive egg laying early in the season probably results in a high rate of cell invasion throughout the season. The moderate parasitism of ***Nomia triangulifera***, which provisions its nests after ***robustum*** adults have virtually disappeared, strongly suggests that parasitic larvae continue to invade cells for several weeks.

Although the first-instar larvae are not attracted to the host larva until it is full grown, they may require some prior nourishment.

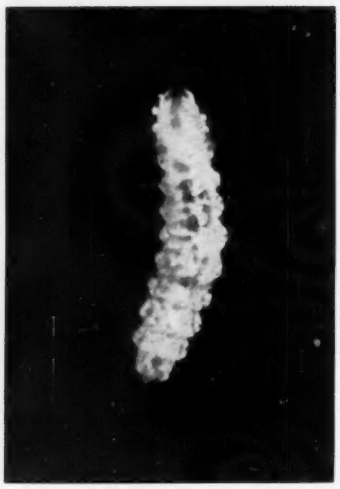

FIG. 8.—Second-instar *Heterostylum robustum*.

According to Nininger (1916), first instars of ***Spogostylum delia*** Loew may feed on a carpenter bee pollen mass for a month before implanting on the mature larva. Recently hatched larvae of ***robustum*** are not attracted to host larvae of any age and, when confined with prepupae, wander about and die within 24 hours at room temperature (75° F.). At lower temperatures (65° F.) they remain active for several days. While its host is defecating and transforming to a prepupa, the primary larva remains on it, but grows only slightly and does not appear to become attached. At this time it may merely feed on exudates and condensed moisture. Nevertheless, some feeding on the host before formation of the prepupa may be required, although the previously mentioned cases of implantation on overwintered hosts indicate otherwise. First-instar larvae of another bombyliid, ***Anthrax fur*** O. S., frequently wait until the overwintered prepupae of its host bee

pupate in May or June before attaching themselves (Linsley and MacSwain 1942).

In the Uinta Basin of eastern Utah several third-instar *Heterostylum* larvae were found on alkali bee prepupae on June 12 before nesting had started. Since no pupal exuviae or ovipositing parasites were found at this date or earlier, it appeared that these larvae had overwintered in the first instar. However, since adults were not collected for identification, it is not certain that the species involved was *robustum*.

FIG. 9.—Third-instar *Heterostylum robustum* feeding on prepupal *Nomia melanderi* in artificial cell.

FIG. 10.—Third-instar *Heterostylum robustum* (ventral aspect and mouth parts).

In Utah two or three first-instar larvae are commonly found on a single host larva (fig. 7), but only one makes significant growth and molts to the next stage. The fate of the unsuccessful larvae has not been determined, but there has been no evidence of combat such as takes place with meloid or clerid larvae.

The larvae usually take their first position lying ventrally or laterally between two thoracic segments (fig. 7). When several parasites are on the same host, some may also be found between the anterior abdominal segments. The first instars do not attach themselves firmly and often change position after starting to feed.

The feeding larva remains in the first instar for about 36 hours, during which time it increases in length from 1.8 to 2.3 mm. and more than doubles in diameter. It is smoothly cylindrical at first, but moniliform when fully distended (fig. 7).

Second instar.—Larvae in the second-instar have only been seen a few times, and they appear to remain in this stage for 12 hours or less. This instar is flattened dorsoventrally with well-marked segments and no caudal filaments (fig. 8). The posterior spiracles are prominent and project over the base of the terminal segment. The little growth in this instar seems to have but slight importance in the larval development. A second instar has not been observed by other authors describing the larval stages of bombyliids. Even Berg (1940), who described in detail the larval stage of *Systoechus vulgaris*, did not observe it. Unfortunately, larvae of this instar were not preserved and now we have only a photograph, some sketches, and notes to verify its existence. It is possible that the instar here described as the second merely represents certain individuals of the instar described below as the third which, for some reason, failed to grow normally for the first 12 hours.

Third Instar.—This instar feeds for 2 or 3 days and grows rapidly, increasing in length from 2.3 to 8.3 mm. and in diameter at least three-fold. This instar has a creamy white, translucent ap-

pearance with many oval, opaque, white fat bodies clearly discernible in the abdomen. It curls around the body of its host and remains attached in one place to the ventral or lateral aspect of the thorax or abdomen (fig. 9). However, it has no difficulty in implanting itself again if its head is moved away from the host.

FIG. 11.—Overwintering fourth-instar *Heterostylum robustum* in its cell.

In this instar the parasite is smooth, soft, and plump, with no bristles or tubercles for locomotion. The concave area around the mouth parts is pressed tightly against the host integument during feeding. This position appears to help the larva develop a vacuum while drawing liquids through the minute wound in the host's body wall. Fabre (1913) failed to observe any mouth hooks in the larvae of *Anthrax* and found no leakage of air when he inflated the emptied skins of host larvae. He assumed that no wound was made and that suction alone accomplished the transfer of fluids. The mouth parts of the third-instar ***robustum***, which are minute (fig. 10), consist of a slender pair of knifelike mouth hooks flanked by blunt, poorly sclerotized maxillae bearing short, naked palpi. The host remains alive and unchanged in color while the larva is feeding, although it becomes noticeably shrunken.

Fourth instar.—In this instar the larva is ventrally flattened, posteriorly tapered, and has a leathery, wrinkled integument, six pairs of bristles on the head and one pair ventrolaterally on each of the thoracic segments (fig. 11). The thoracic bristles articulate freely at the base and probably assist the larva in locomotion. There are no bristles on the caudal segment. This instar also has flat, wartlike knobs on each body segment

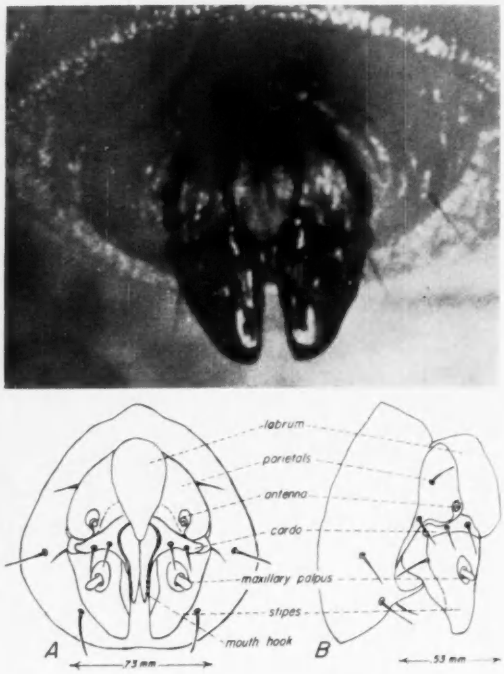

FIG. 12.—Mouth parts of fourth-instar larva of *Heterostylum robustum*.

and 13 slightly more prominent protuberances on the caudal segment. The numerous transverse wrinkles on all body segments serve to strengthen the body wall and allow for expansion. As the larva becomes distended, the wrinkles smooth out, but they remain sufficiently prominent to assist in locomotion.

The mouth parts at this stage are conspicuous and well sclerotized with a pair of median swordlike mouth hooks flanked by broad, heavy, shieldlike maxillae bearing small, peglike palpi on broad basal plates (fig. 12). The head has a peculiar hornlike labrum extending forward over the base of the mandibles. The respiratory system is similar to that of the third instar, with spiracles on the prothoracic and penultimate abdominal segments.

The larva readily releases its hold on the host when disturbed, but immediately fastens to it

again with its maxillae and penetrates the integument with its mouth hooks. It readily attacks a new host and takes wasp or honey bee larvae without hesitating (fig. 13). If several parasites are placed in a container, they become cannibalistic.

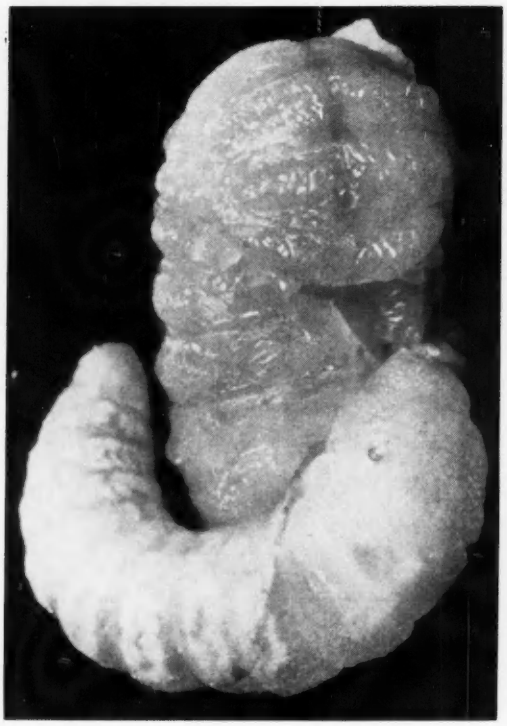

FIG. 13.—Fourth-instar larva of *Heterostylum robustum* shedding third-instar skin and feeding on *Tachysphex* prepupa.

The fourth instar feeds for 3 or 4 days and increases in length from 8.5 to 16 mm. In the laboratory in 1 day it consumes the fluids from the first host larva and then starts searching for another host. It readily feeds on another host larva but does not completely drain it unless it is considerably smaller than an alkali bee larva. Field observations in Utah indicate that the fourth instar commonly drains the first host and about half of the second. As it leaves the first cell, it plugs it tightly with dirt, sandwiching the empty host skin between the plug and the cell wall. It then burrows through the soil, filling the tunnel behind it until it finds another cell containing a prepupal bee. Within 2 days it drains this bee of about half its contents and leaves its cell. The half-eaten host larva is jammed against the cell wall with a loose plug of dirt (fig. 14). After draining the fluid from the first host, the parasite weighs 0.13 to 0.16 mg., and when full-grown it weighs 0.19 to 0.22 mg. It seems to be a remarkable feat for the parasite to complete its development on a single alkali bee prepupa (which weighs 0.126 to 0.198 mg.), but observations in Oregon indicate that this is normal in that area. Evidence for a consistent 1:1 ratio in

FIG. 14.—Half-eaten second host larva (*Nomia melanderi*) with exit tunnel of *Heterostylum robustum* at the side.

Oregon consisted of an absence of partially consumed larvae or of last-instar parasites feeding on plump host larvae. The larvae increase their weight during the growth period approximately 458 times (from 0.0005 to 0.228 mg.).

Overwintering.—The full-grown larva burrows laterally and upwards from the brood chamber at the 5- to 10-inch level until it reaches a point 2 to 3½ inches below the soil surface. Here it excavates a large, roughly oval overwintering cell. Many genera of hymenoptera-parasitizing bombyliids do not leave the host cell (e.g., *Anthrax*, *Toxophora*, *Poecilanthrax*), and have soft, relatively helpless last-instar larvae (Fabre 1913). *Bombylius*, like *Heterostylum*, leaves its host cell and has a tough, active last instar. However, the last instar of *Bombylius* is whiter than that of *Heterostylum* and not as rough in texture.

The *robustum* larva overwinters in a C-shaped position, either horizontally on its side or with

the anterior end directed downward (fig. 11). It is quiescent during this period, but when disturbed can straighten out and curl again without difficulty. Although some overwintering larvae can be found at a depth of 10 inches, these appear to be individuals that matured late in the season

FIG. 15.—Pupa of *Heterostylum robustum*.

FIG. 16.—Adult *Heterostylum robustum* emerging from its pupal skin.

after soil temperatures dropped. It was observed in Oregon that a larva deep in the soil makes its way to the upper few inches before pupating in the spring. No evidence has been observed of a mature *Heterostylum* larva remaining in the soil more than one year, but the senior author has seen many 2-year-old larvae of *Bombylius* as a parasite of *Halictus farinosus* Cress.

PUPAE

It is presumed that pupation takes place within the overwintering cell if it is sufficiently shallow. In the laboratory mature larvae have been seen to hollow out overwintering cells in plaster of Paris and pupate within them. The pupa (fig. 15) is white at first, but within 2 days it becomes yellowish brown, and a week later it turns darker as the adult forms within the pupal skin. As the pupa darkens it becomes very active, rotating whichever end is free and alternately extending and telescoping its abdominal segments. Structurally it is well equipped to drill and push its way through the soil. Its head is provided with three pairs of long backward-curved spines, and it has a double-bladed shovel-like structure at the base of the mouth parts. There is a pair of stout hooklets near the base of its wings, and each abdominal segment has a prominent circle of alternating hooks and long, strong bristles. Finally, its posterior segment is provided with a pair of long, sharp spines and several shorter ones. Fabre (1913) described the manner in which *Anthrax* pupae break through their confining walls. Kunckel d'Herculais (1905), in discussing the emergence of *Systropus* from eucleid cocoons, described the ability of the pupa to fill its digestive tract with air, thus inflating its body and bringing greater pressure to bear with the cutting structures on its head.

The pupa of ***robustum*** embeds the hooks of its head capsule into the upper part of its pupal cell and, by gyrating the abdomen, packs loose soil beneath it. Its anterior end is then gyrated, resulting in an excavation of the soil above it. This process is repeated until the pupa reaches the soil surface. The soil crust is broken and pushed back, and a few moments later the pupal head is visible, rotating back and forth about a

quarter of a turn. With each rotation the abdominal segments expand and contract in rhythmic waves. This activity soon forces the head and thorax clear of the ground. The upward motion of the pupa then ceases, and in less than a minute its thoracic skin splits down the back. As the split extends to the base of the head, the adult fly forces its way upward and out of the pupal case (fig. 16). It remains for a few minutes with the rear portion of its abdomen still in the case while the mouth parts, and finally the legs, are extended away from the body. It then drops forward onto its fore and mid legs, kicks itself free of its case with its hind legs, and crawls along the ground with its straplike wings slowly expanding. It mounts the first clod or stem it encounters and hangs with its head up to dry. As the wings expand and harden, droplets of fluid are released from the anus. Within 10 minutes the adult is ready to fly, but it remains for several minutes more if undisturbed.

During the period of emergence and hardening, the flies are very vulnerable to predators. In northern Utah and in Oregon blackbirds, magpies, meadow larks, and English sparrows have been seen to feed on them, and there are probably many other bird predators. Although these birds feed on bees and flies alike, it is suspected that the flies, because of their initial sluggishness, are fed upon to a greater extent than the bees.

The pupal exuvium is usually anchored in the soil by its posterior half, and in compact, fine-grained soil it often remains intact and conspicuous for the remainder of the season. In such areas the presence of ***robustum*** in the nesting sites of bees can be determined most easily by looking for pupal exuviae. However, if the soil is sandy or loose at the surface, the wind soon loosens the pupal cases and blows them into windrows.

MATING

Mating usually takes place on the vegetation surrounding the site. However, in Oregon males were observed on several occasions to mate with newly emergent females on the nesting site. In one copulation observed in Utah the female was holding onto an upright stem with all three pairs of legs, and her body was inclined away from the stem at an angle of about 45 degrees. The male was facing away from the female with his body nearly horizontal and the tip of his abdomen bent upward to make contact at the proper angle. The female was motionless with her wings extending posteriorly in a resting position, but the male held his wings outstretched and intermittently fluttered them slightly. This mating was observed to last for 15 minutes, but the beginning of contact was not seen. The males do not pursue females over the *Nomia* burrows, although they can be seen hovering over the nesting area. Search for females apparently takes place in the morning before they are active over the nests and also in the afternoon when they take shelter in the surrounding vegetation.

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ADDENDUM TO A REVIEW OF THE GENUS OMALUS PANZER IN NORTH AMERICA (Hymenoptera, Chrysididae)

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In our paper on *Omalus* (Ann. Ent. Soc. America 53: 235–50) Dr. L. E. Campos and I inadvertently omitted the description of *O. plicatus* (Aaron), although figures were given, and it was included in the key. The species belongs to the subgenus *Diplorrhos* Aaron, and the toothed second abdominal tergite is diagnostic. Altogether, 42 males and 219 females have been studied from a large geographical area including Alaska, Canada and the western and northern parts of United States proper. Borderline states are New Mexico, Minnesota, Michigan, and New York. The taxonomic history is as follows:

Diplorrhos plicatus Aaron, 1885. Trans. Amer. Ent. Soc. 12: 216. Montana (♀ lectotype, ANSP).

Omalus plicatus (Aaron) of Bohart and Campos, 1960. Ann. Ent. Soc. Amer. 53: 236.

EXTENDED DIAPAUSE IN EGGS OF HIGH-ALTITUDE SPECIES OF GRASSHOPPERS, AND A NOTE ON FOOD-PLANT PREFERENCES OF MELANOPLUS BRUNERI[1]

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ABSTRACT

To investigate the possiblity that their eggs require more than a year for development on high-altitude rangeland in the northern Rocky Mountain region, adults of *Melanoplus bruneri* Scudder, *M. borealis* (Fieber), *M. alpinus* Scudder, and *Chortippus longicornis* (Latreille) were caged on their native habitat. After 2 years, the eggs found in the soil under the cages were brought into the laboratory. A short period of incubation caused all the eggs of *borealis* to hatch, but more than half those of the other species failed to do so. An additional cold period was necessary to break the diapause in the remaining eggs. Nymphs and adults of *bruneri* fed heavily on lupine and timothy, and damage to timothy became especially noticeable as lupine became depleted. Many plant species in the habitat were ignored as food sources.

Most grasshoppers complete their life cycles in 1 year, but a few species have been reported to require 2 years. Pickford (1953) found that *Pardalophora apiculata* (Harris), *Xanthippus latefasciatus* Scudder, *Arphia conspersa* Scudder, *Chortophaga viridifasciata* (DeGeer), and *Psoloessa delicatula delicatula* (Scudder) usually pass the first winter in the egg stage and the second in one of the later nymphal stages in central Saskatchewan. Recently Putnam and Handford (1958), after observing that high populations of *Melanoplus bivittatus* (Say) occurred in alternate years in British Columbia, found that diapause in the eggs prevented most of them from hatching until two winters had been passed, although this insect has only a 1-year cycle in Saskatchewan. These authors also indicated that *M. bruneri* Scudder and *M. borealis junius* (Dodge) may have similar life cycles.

In 1952 erratic results were obtained in a grasshopper control campaign in the Big Horn National Forest, Wyoming. Four high-altitude species were principally involved: *Melanoplus borealis* (Fieber), *M. bruneri*, *M. alpinus* Scudder, and *Chorthippus longicornis* (Latreille). Seaton (1954) reported that during the year following control operations many reinfestations occurred which could not be explained on the basis of poor kill or adult migrations after spraying. A study was therefore made to find out whether diapause eggs deposited the year before control operations were undertaken could have caused these reinfestations if they remained in the soil for 2 years before hatching.

DIAPAUSE STUDIES

In the summer of 1954 adults of the four species were caged on the Big Horn Mountains at an elevation of 8,500 feet. Grasshoppers were separated to species, and the cages were placed over ground from which the sod had been removed to eliminate egg pods of unknown age. The insects were fed daily throughout the summer, and by September sampling revealed good oviposition in all cages. During the summer of 1955 the cages were kept under observation but were not disturbed. On June 5, 1956, the egg pods were removed from the soil under each cage and brought into the laboratory at Bozeman, Montana. Some of them were incubated at 85° F. and the others were held in cold storage at 37°.

In 1955 a similar experiment was undertaken on the east slopes of the Crazy Mountains, Montana, but unfortunately no oviposition occurred. In the summer of 1956 a population of *M. bruneri* and *C. longicornis* was located on the west slopes of the Crazy Mountains, and caging resulted in the acquisition of a few pods of *bruneri* only. These egg pods were permitted to remain under the cages until the spring of 1958, when they were brought into the laboratory and incubated as before.

Results of incubating the eggs in the laboratory after 2 years' development in the soil are shown in table 1. A complete hatch was obtained only of *borealis*. Examination of the unhatched eggs of the other three species revealed fully developed, resting embryos; so it was suspected that either the diapause was still unbroken or a longer period of incubation was required. After a month of incubation it was decided that no further hatching would take place.

In order to simulate a third winter, the unhatched eggs were placed in a refrigerator at 37° F. on July 7 and allowed to remain there until November 5, after which they were reincubated as before. Within a few days after reincubation, the remaining eggs of the three species hatched,

[1]Accepted for publication October 19, 1959.

[2]W. E. Booth, Professor of Botany, Montana State College, confirmed the plant identifications, and Lee Seaton, then with this Division, did the preliminary work which made possible the collection of most of the eggs used in this study.

Table 1.—Hatching data from eggs of four high-altitude species of grasshoppers incubated at 85° F. after 2 years' development in the soil. 1956.

Species	Number of pods	Incubation period	Hatching period	Degree of hatch
Melanoplus borealis	20	June 6–10	June 6–9	Complete
Melanoplus bruneri	20	June 6 to July 7	June 11–15	Incomplete
Melanoplus alpinus	15	do.	None	Only 1 hatched
Chorthippus longicornis	20	do.	June 11–16	Incomplete

indicating the likelihood of a 3-year developmental period.

When the egg pods were brought into the laboratory and incubated, the fact that some of the eggs might still be in diapause was unanticipated. For this reason, the exact numbers of eggs incubated of each species were not determined. In order to obtain rough estimates of the numbers of eggs of each diapause type, the egg pods that were refrigerated upon their removal from the soil were used. The pods of each species were broken and the eggs counted. After incubation at 85° F. the immediate hatch was as follows:

Species	*Number of Eggs*	*Percent Hatched*
M. bruneri	230	40
C. longicornis	75	28
M. alpinus	48	8

The remaining eggs hatched after an additional cold period.

According to these data, most of the eggs of *alpinus* and *longicornis* require a 3-year developmental period, but those of ***bruneri*** seem to be more evenly divided between the 2- and 3-year types. These findings explain the failure of control campaigns involving these species.

Upon incubation, eggs of ***bruneri*** obtained on west slopes of the Crazy Mountains hatched completely without the application of an extra cold period, in contrast to the eggs collected at the Wyoming location. It may be significant that the Montana location is about 2,500 feet lower than that in Wyoming, although the fact that very few egg pods were obtained cannot be ignored. The possibility that the difference might be due to laboratory conditions was only slight, since there was no effect on the hatch of ***borealis***.

Slifer (1931) reported that although obligatory diapause occurs in most eggs of ***Melanoplus differentialis*** (Thom.) a small percentage develop without interruption and this absence of diapause may be inherited. Perhaps the differences in length of diapause in ***bruneri***, ***alpinus*** and ***longicornis*** have a genetic basis also. Slifer (1946) later showed that diapuse eggs of ***differentialis*** resumed development after treatment with solvents that removed a water-impermeable layer of wax on the hydropyle. Eggs of ***bruneri*** treated similarly failed to break diapause.

FOOD-PLANT PREFERENCES OF *Melanoplus bruneri*

Feeding preferences of ***bruneri*** were observed in conjunction with diapause studies. This species was selected because of the frequency with which it is found on moderate- to high-altitude rangelands. Individuals were watched under natural conditions in a meadow on the west slopes of the Crazy Mountains. Both nymphs and adults were observed from early June until late in August. The adult population at the height of the season was approximately 15 per square yard.

Eight plants were readily fed upon, although not all at the same time (table 2). Populations of this grasshopper have been observed to thrive

Table 2.—Food plants of *Melanoplus bruneri*, in decreasing order of preference.

Plant	Time fed upon	Parts eaten
Lupinus sericeus	June, July	Flowers, leaves, stems
Phleum pratense	June, July, August	Heads, leaves
Achillea lanulosa	June, July, August	Flowers
Thelypodium sagittatum	July	Flowers, leaves, stems
Carum carvi	August	Flowers
Erigeron subtrinervis	June, July	Flowers
Geranium viscosissimum	August	Leaves
Bromus marginatus	June, July	Heads, leaves

in weedy habitats in which *Lupinus sericeus* (lupine) is usually one of the dominant plants.

The first plant to show extensive damage was lupine, on July 15. About a week later, when nearly all the population had reached adulthood, lupine was almost completely defoliated. At this time damage to leaves and heads of *Phleum pratense* (timothy) and heads of *Achillea lanulosa* (yarrow) was becoming much more noticeable. Extensive feeding on these two plants continued until dryness made any feeding difficult to observe. On August 13 many individuals were utilizing *Geranium viscosissimum* (sticky geranium) for food. This plant had been completely ignored during most of the season and was utilized only when other vegetation became desiccated.

In general, *bruneri* was observed to feed primarily on lupine, but turned its attention to timothy after most of the lupine was depleted. Timothy, an important grass on the study area, was the only grass on which prolonged feeding occurred.

Plants that were common in the environment but ignored as sources of food are listed below.

Dicots	Monocots
Eriogonum umbellatum	*Agropyron subsecundum*
Senecio sp.	*Agropyron bakeri*
Arnica rydbergii	*Agropyron trachycaulum*
Geum triflorum	*Festuca idahoensis*
Potentilla gracilis	*Poa cambyi*
Anaphalis margaritacea	*Melica spectabilis*
Collomia linearis	*Stipa columbiana*
Gaillardia aristata	*Koeleria cristata*
Campanula uniflora	*Danthonia unispicata*
Polygonum bistortoides	*Carex petasata*
Arenaria congesta	*Zygadenus venenosus*
Sedum douglasii	
Taraxacum sp.	

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ANNUAL MEETING

ENTOMOLOGICAL SOCIETY OF AMERICA

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SCIENTIFIC NOTES

The Oviposition of *Enallagma exsulans* (Odonata: Agrionidae)[1]

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Walker (1953), concerned with *Enallagma exsulans*, stated that "ordinarily oviposition takes place in beds of submerged aquatic plants after the manner of most enallagmas, but Calvert (1893) observed three ovipositing pairs of *exsulans* descend below the surface of the water." The fact that most enallagmas oviposit at or near the surface of the water is confirmed by Walker's general comments concerning different species of *Enallagma*. Statements such as "among floating *Utricularia*," "at the surface," "just below the surface," and "a little above water level" point out this behavioral characteristic. Calvert (1893) said in effect that when a female deposits eggs below the water surface, she must of course be partly or wholly covered by the water, and if and when the female descends so far as to begin to pull the male, with which she is in tandem, into the water, he usually releases hold and separates from her to avoid being dragged beneath the surface. Calvert mentioned, however, that he saw on three occasions, males and females of *E. exsulans* descend in tandem into the water until submerged.

I observed a tandem pair descend to a depth of about 15 inches below the water, and since this seemingly is of uncommon occurence, I believe it worthwhile to describe the event here. This observation was made on July 17, 1959, at Fleming Creek, a small woodland stream with heavy vegetative cover and much emergent vegetation in season, on the property of the University of Michigan Botanical Gardens, Washtenaw County, Michigan. The day was sunny and warm, the water temperature 18° C., and a current velocity of 10–12 cm./sec. was measured at the point of observation.

A male and female were observed to alight in tandem on a filament of *Potamogeton filiformis* rooted in about 15 inches of water and floating out on the surface with the current. The female moved about slowly over many filaments, probing backwards with the tip of her abdomen, seemingly in an effort to find a suitable strand upon which to oviposit. After many probes with the tip of her abdomen beneath the surface of the water, a strand was selected and oviposition began. Although the number of eggs laid was not counted, the ovipositing continued down the filament in the following repetitious manner. The female probed about with the tip of her abdomen, deposited an egg, grasped the vegetative strand at that point with her terminal abdominal appendages, and backed down the filament as far as possible in that position. She then released the grasp with her forceps and began again to probe for a place to deposit an egg. Once this was accomplished, she regrasped the plant and backed down the filament as before. Oviposition thus continued until the stream bottom was reached. It was actually not obvious to me whether oviposition preceded the grasping of the filament with her terminal appendages or whether oviposition occured while it was so held. Descent, however, began very shortly after the grasping of the filament with the terminal appendages.

During this period of time the male seemed to be a passive and clumsy "tag-along," as the female, with all the initiative, pulled him in whichever direction she wished.

Once at the bottom, continued probing with the tip of her abdomen for another place to deposit an egg found nothing but the silt of the stream bed. Then, after being submerged for 17 minutes, and without apparent movement, warning, or communication, both male and female released their holds simultaneously and, still in tandem, popped to the surface like a cork. Breaking the surface film, they floated upon it for a few seconds and then flew to an emergent piece of vegetation where rapid ventilation followed. After ventilating for no more than a minute, they flew off, still in tandem.

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A Comparative Study of the Free Amino Acids and Carbohydrates of the Pink Bollworm, *Pectinophora gossypiella*[2]

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The use of paper chromatography as a taxonomic tool in insect studies has increased greatly since Clark and Ball (1951, 1952), Ball and Clark (1953), and Micks and Ellis (1951, 1952) first used the technique to seek inter- and intraspecies differences, and has been recently reviewed by Micks (1956), Micks and Gibson (1957), and Robertson (1957). A study was made to determine whether there are any appreciable differences in free amino acid and carbohydrate content between the diapaused and nondiapaused fourth-instar larvae of the pink bollworm, *Pectinophora gossypiella* (Saund.), using paper chromatographic methods.

Procedure.—Homogenates of eggs and moths, and haemolymphs of fourth-instar nondiapause larvae, fourth-instar diapause larvae, and pupae were each analyzed chromatographically. Each sample consisted of a homogenate of 40 to 200 eggs or 10 to 12 adults, or 100 µl. of pooled haemolymph taken from incisions in the prolegs or integument of 10 to 12 larvae or pupae. The sample was deproteinized by adding cold 85% ethanol to give a final concentration of 50% alcohol, and the resulting precipitate was removed by centrifugation. The precipitate was subsequently washed and centrifuged twice with 50% ethanol, and the supernatants were pooled with the first supernatant. To concentrate the sample, the ethanol supernatant was then shaken with three volumes of chloroform to remove the ethanol, allowed to separate, and the aqueous phase removed for chromatographic analysis. The amount placed on the chromatographic paper represented 20% to 50% of the original sample volume.

Qualitative amino acid analyses were carried out by means of the two-dimensional ascending paper chromat-

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[3]In cooperation with the Texas Agricultural Experiment Station.

Table 1.—Free amino acids, amines, and other ninhydrin-reacting compounds in the haemolymph and whole body extracts of the pink bollworm. (Distinct spots 1, faint spots 2, not detected 3)

Compound	Eggs	Fourth-Instar Larvae		Pupae	Adult
		Nondiapause	Diapause		
α–Alanine	1	1	1	1	1
β–Alanine	3	1	1	1	2
γ–Aminobutyric acid	3	3	3	2	3
α–Amino-n-butyric acid	3	3	2	2	2
Arginine	1	1	1	1	1
Asparagine	3	3	3	2	3
Aspartic acid	2	2	2	3	3
Cysteic acid and/or cysteine	3	2	2	2	2
Glucosamine	2	3	2	3	3
Glutamic acid	1	1	1	1	1
Glutamine	1	1	1	1	1
Glutathione	2	2	2	3	2
Glycine	1	1	1	1	1
Histamine	3	3	3	2	2
Histidine	1	1	1	1	1
Hydroxyproline	3	3	3	3	3
Isoleucine and/or leucine	3	1	1	2	2
Lycine	1	1	1	1	1
Methionine	1	1	1	1	1
Methionine sulphoxide	1	1	1	1	1
Peptides	3	1	1	1	1
Phenylalanine	2	2	2	2	3
Proline	3	2	2	2	2
Serine	1	1	1	1	1
Taurine	3	2	3	2	3
Threonine	1	1	1	1	1
Tryptophane	1	1	1	1	1
Tyrosine	3	1	1	1	2
Unknown compounds	3	3	3	2	2
Valine	1	1	1	1	1

ographic technique (Williams and Kirby 1948). The solvents used consisted of phenol (saturated with water), 2,4-lutidine (75%), and, following Bentley and Whitehead (1950), propanol (70%) or acetone (60% with 1% w/v urea). The separations were carried out on both 6×6 and 15×15 inch sheets of Whatman No. 1 filter paper. The papergrams were dried at room temperature rather than high temperatures to prevent qualitative and quantitative errors due to phenol-induced heat lability of α amino acids (Brush 1951). Visualization of the spots was accomplished by spraying the paper with ninhydrin (0.2% w/v) and 1% acetic acid in n-butanol (Consden et al. 1948). Twenty most common amino acids and amides were chromatogrammed to determine the R_f values and to establish reference chromatographic maps. The chromatographic maps shown by Dent (1948) and the R_f values found by Clark and Ball (1952) were also used as references. If it was questionable whether a spot represented an amino acid or a peptide, the supernatant was divided into two portions, one of which was hydrolyzed by refluxing it with 10 volumes of 6N hydrochloric acid at 130° C. for 6 hours, and then compared chromatographically with the unhydrolyzed portion. Histidine was identified on the paper with diazotized sulfanilic acid (Pauly 1904) and arginine by a slight modification of the Sakaguchi reaction (Sakaguchi 1925). Relative amounts of the amino acids were made by visual inspection based on the size and intensity of the chromatographic spots.

Carbohydrates were analyzed by one-dimensional ascending chromatography. The solvent used was either phenol (saturated with water) or butanol-acetic acid-water (4:1:5 v/v) (Partridge 1948). The sugars were visualized by spraying the paper with a beta-naphthylamine reagent (Novellie 1950). Identification was carried out by comparing knowns and unknowns chromatogrammed simultaneously.

Results. The results of these analyses for free amino acids, amines, and related ninhydrin-reacting compounds are found in table 1. Fructose and glucose were present in all stages of the pink bollworm. Detectable amounts of glucose-1-phosphate were found in the eggs and fructose-1, 6-diphosphate in the fourth-instar larvae.

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An Abnormal Grasshopper With Two Median Ocelli (Orthoptera, Acrididae)[1]

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Among a number of grasshoppers caught near Iowa City in October 1957 a male *Melanoplus differentialis differentialis* (Thomas) with two median ocelli was found. The unusual condition was not noticed until the head had been removed for experimental work and the cut cervicum had been sealed with vaseline. Several hours later the head—still alive as indicated by the movements of mouth parts and antennae—was placed in 70 percent alcohol to which a little formalin had been added.

A search of the literature has produced two papers in which grasshoppers with a pair of median ocelli have been reported. Blackman (1912) described a female *Melanoplus femur-rubrum* as follows: "The two median ocelli [are] placed symmetrically one on each side of the median line. Each is approximately circular and apparently perfect in every respect. Each one as far as could be observed is but slightly smaller than the single ocellus usually is. The two are entirely distinct, each being set in a slight depression with the intervening distance greater than the diameter of each ocellus." Blackman prepared serial paraffin sections of the head and found that the ocellar pedicel—or ocellar nerve, as he called it—left the brain as a single structure and branched into two before joining the ocelli. The material was too poorly fixed to show cellular details. A specimen of *Melanoplus differentialis* with two median ocelli was found by Glasgow in 1925. He did not record its sex. In Glasgow's words: "In this specimen the lateral ocelli are normal in position, in form, and in size. The median ocellus, however, is represented by two perfectly formed ocelli which are disposed symmetrically, one on each side of, and laterad from the point where the normal median ocellus should be, and separated from each other by a distance somewhat greater than the diameter of a normal median ocellus. Each of these paramedian ocelli presents the characteristic oval form of a normal ocellus, each has a characteristically distinct, convex cornea, and each is situated in a separate characteristically oval depression in the front; but these aberrant ocelli are somewhat smaller than normal, so that the two ocelli

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FIG. 1.—Anterior view of head showing two median ocelli. × 11.

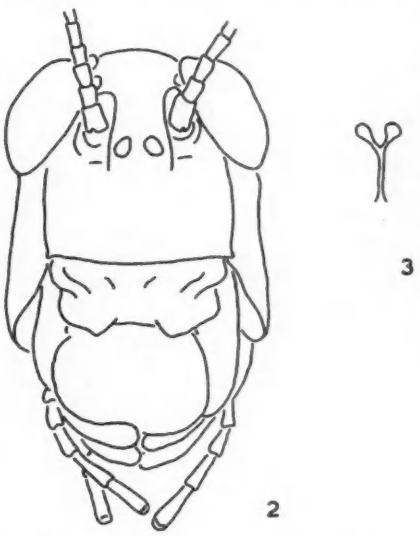

FIG. 2.—Anterior view of head. × 9.

FIG. 3.—Ventral view of ocellar pedicel and two ocelli after dissection from head. Brain, to which pedicel is attached, not included in drawing. × 9.

together would present an aggregate area but little if at all greater than the area of a normal median ocellus." The specimen was too badly preserved to permit study of the internal organs.

The descriptions given by Blackman and by Glasgow, with one important exception, would serve almost equally well for the male which is the subject of the present paper. Each of the ocelli of this individual is as large as a normal median ocellus. In figures 1 and 2 it will be noticed that the frontal carinae are bowed outwards somewhat more than is usual as they pass the two ocelli. Moreover, the diameter of each ocellus is very nearly the same as the diameter of the basal portion of the antennal flagellum. Examination of the photograph in Glasgow's article shows that each ocellus in his specimen had a diameter much less than that of the flagellum. The same is true for the female *Melanoplus femur-rubrum* shown in Blackman's photograph.

After the external parts of the head had been studied the brain, together with the ocellar pedicel and ocelli, was dissected out, sectioned in paraffin and stained with Mallory's triple connective-tissue stain. The median ocellar pedicel, as in Blackman's individual, left the brain as a single structure and branched just before joining the inner surface of the ocelli (fig. 3). That portion of the pedicel which contains the giant fibers was single but the region where the delicate axons from the retinal cells synapse with the giant fibers was double; that is, there were two complete ocellar centers. Sections of the two ocelli were compared with sections of a median ocellus from a normal male of the same species. Each of the two resembled the normal ocellus so closely that no differences in the types of cells present, their size, number or arrangement could be detected.

Thanks are due to Dr. Robert L. King who took the photograph which is reproduced in figure 1.

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BOOK REVIEW

LAND AND WATER BUGS OF THE BRITISH ISLES, by T. R. E. Southwood and D. Leston. Frederick Warne & Co. Ltd. London. 1959. 5 x 7 inches, 436 pp., 32 col. plates, 31 black and white plates, 153 text figs. 30 shillings.

This is the first comprehensive book on British Hemiptera since 1892 and the first "Biology" since 1923. It takes its place with such classics as Douglas and Scott's "British Hemiptera" (1865) and Saunders' "Hemiptera Heteroptera of the British Islands" (1892). It is interesting to note that the number of known species increased from 355 in 1865 to 442 in 1892 and 509 in the present work. But numbers are the least significant of the advances made in this book. The British fauna has been studied more intensively and more enthusiastically than that of any other comparable area of the world. The reasons for this are complex and but little understood but the facts are clear. Nowhere in the world, with the possible exception of Japan, has there been such widespread interest and devotion to insect collecting by scholarly amateurs. The present book, though thoroughly professional as to scientific facts, has caught this spirit. In style and method of presentation it is a fitting addition to the charming "Wayside and Woodland Series." The beautiful colored plates, clear printing and attractive binding would price the book out of its market in may places. In fact, the $4.20 price seems to belong to another economic era.

The detailed treatment of species is far superior to that in the companion volume "Flies of the British Isles" by Colyer and Hammond for the obvious reason that it is easier to deal with 500 species than 5000. The authors have done an excellent job of summarizing previous knowledge and integrating their own extensive observations. A unique contribution is the inclusion of chromosome numbers of species, about 70 resulting from the authors' own studies.

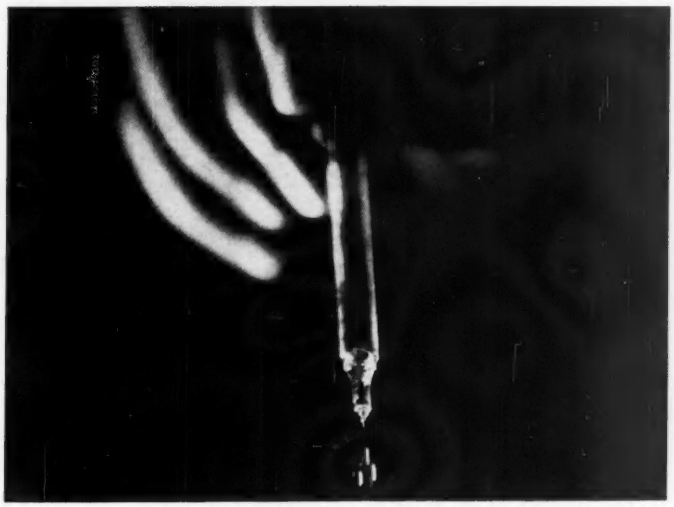
From the viewpoint of an occasional student of the British fauna who needs a handy reference, the book has certain shortcomings in format. There are no original references, dates, or synonymy at the species level and no generic descriptions, types, authors or dates. However, this information is well known and readily available for the British Hemiptera. Still, it's inclusion would have added little to the size of the book and much to its usefulness.

The authors are well aware of my disagreement on the status of certain families and subfamilies through lively personal discussions. Nevertheless, I feel obliged to publish a protest lest it be assumed that I have been won over to their views. I feel first that controversial decisions should be avoided in a popular book where there is no opportunity to defend the position taken. As regards family status, I feel that it is misleading to follow one classification, such as Aradidae and Aneuridae or Naucoridae and Aphelocheiridae, for the British fauna when subfamily status has been established on the basis of the world fauna. It could, of course, be argued that the level is arbitrary and does not alter the actual relationships of the groups concerned. However, the authors have not even been consistently arbitrary, the Aradid and Naucorid groups having been split or moved upward whereas the Saldid-Aepophilid and Cimicid-Anthocorid groups were down-graded against all current practice.

The book is neatly and reasonably arranged into 14 chapters, the first being an introduction and key to families and the remaining chapters each covering a family, part of a family or a group of closely related families. In each case frankly artificial keys are given down to the species. The keys are clear, consistent, and well illustrated by key characters in the text figures. Each chapter is fully documented with superscript numbers referring to a full and annotated section on "Literature Cited." In this the authors show an intimate and up to date knowledge of the world literature that is not to be found in any recent work on Hemiptera. The first appendix gives the best instructions for collecting and studying Hemiptera that has ever been published. The short glossary serves a useful purpose and appendix 3, "List of Plants and Associated Bugs" is doubtless of considerable use locally.

The authors and publishers are to be congratulated for producing such a sound and comprehensive yet delightful and stimulating book. It will be indispensible for students of the British fauna and is the most convenient and inexpensive source of reference for specialists elsewhere in the world.—

Robert L. Usinger
University of California



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VOLUME 1, NUMBER 1, pp. 1–32 appeared October 1, 1959, and contains the symposium papers on Insecticide Resistance in Arthropods of Medical and Veterinary Importance given at the Salt Lake City meeting in December 1958. Authors are H. F. Schoof, R. B. March, A. W. A. Brown, and Herbert Knutson.

VOLUME 1, NUMBER 2, pp. 33–68 appeared February 17, 1960 and contains a "Phylogenetic-Systematic Study of Larval Oedemeridae (Coleoptera)" by Jerome G. Rozen, Jr.

VOLUME 1, NUMBER 3, is now in preparation. It will contain the following: "A Revision of the Genus *Chlaenius* Bonelli (Coleoptera, Carabidae) in North America," by Ross T. Bell. "Swarming and Mating in Mosquitoes," by Erik Tetens Nielsen and James S. Haeger.

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